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Effects of Protection on Predatory Fish Populations: Ecological Mechanisms and Implications for Management

Efectos de la Protección sobre las Poblaciones de Peces Depredadores: Mecanismos Ecológicos e Implicaciones para la Gestión

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RESUMEN

Los ecosistemas marinos sufren numerosas perturbaciones antrópicas. Entre ellas, la destrucción de hábitats, la contaminación, la introducción de especies alóctonas o el cambio climático generan importantes cambios en la estructura y funcionamiento de los ecosistemas, lo cual tiene repercusión a su vez en los servicios prestados por estos y de los que dependen las sociedades. Uno de los impactos más importantes en el medio marino es la sobrepesca. Las capturas totales han aumentado desde el año 1970 para toda las especies de interés comercial, y actualmente el 90% de los stocks de peces se encuentran sobreexplotados o agotados. Consecuentemente, muchas poblaciones de peces se encuentran amenazadas, la talla media de las especies ha disminuido y la diversidad genética se ha reducido. Todos estos impactos suponen una importante amenaza sobre los ecosistemas marinos y las formas de vida asociadas al mar. Por ello, una gestión y conservación efectiva del medio marino es esencial para la preservación y restauración de los recursos marinos y los ecosistemas.

Las Áreas Marinas Protegidas (AMPs) son reconocidas como una de las herramientas más efectivas para la conservación de la biodiversidad y la gestión de la pesca. Las AMPs consisten en la delimitación de un área en la que las actividades están reguladas, particularmente la pesca. Las AMPs, y en concreto las zonas de reserva integral, donde todos los usos están prohibidos, son ampliamente reconocidas como zonas efectivas para la conservación y recuperación de las poblaciones de peces, y para reducir numerosos impactos antrópicos. Entre sus beneficios, se espera que aumenten la abundancia y biomasa de peces, así como la capacidad reproductiva de los mismos, ya que los animales de mayor tamaño producen desproporcionadamente mayor número de larvas, y además estas tienen mayores tasas de supervivencia. Además, se espera que las AMPs beneficien las zonas adyacentes mediante procesos de desbordamiento (“spillover”) mejorando las pesquerías locales. Al eliminar el esfuerzo pesquero dentro de las reservas se espera que se produzca una mejora en la calidad del hábitat, repercutiendo positivamente en las poblaciones de peces. Además, ha sido demostrado que las AMPs aumentan la resiliencia frente al cambio climático y otras perturbaciones humanas. Por todo esto, las AMPs han sido propuestas como medidas de gestión efectivas de bajo coste para mitigar los efectos antropogénicos. Sin

embargo, los efectos de las reservas parciales, en las cuales algunos usos están permitidos, no son tan evidentes. Algunos autores han sugerido que las reservas parciales son menos efectivas que las reservas integrales, especialmente cuando las especies que pueden ser capturadas en estas zonas parcialmente protegidas (o tampón) son las mismas que las que son protegidas en la reserva integral. Sin embargo, estudios recientes han demostrado que las reservas parciales bien reguladas, bien vigiladas y localizadas cerca de zonas de reserva integral pueden ser muy efectivas ecológica y económicamente. Por lo tanto, es necesario entender los efectos locales de las reservas parciales para determinar su efectividad tanto para los recursos marinos como para las comunidades que viven de ellas.

Actualmente hay más de 11 000 AMPs designadas en todo el mundo. Sin embargo, a pesar de ser una cifra alta, representan solo un 4.8% de la superficie de los océanos mundiales, y aún así una buena parte de esas AMPs aún no están implementadas o están todavía en fase de propuesta. Aproximadamente la mitad de esas AMPs cuentan con zonas de reserva integral. A pesar del aumento en el establecimiento de AMPs en las últimas décadas, la proporción de áreas protegidas es insuficiente para alcanzar el objetivo 11 de los Objetivos de Biodiversidad de Aichi (Convención de Biodiversidad Biológica), por el cual al menos el 10% de las áreas marinas y costeras deben estar protegidas de una forma eficaz para el año 2020. Más recientemente, la Unión Internacional para la Conservación de la Naturaleza (Hawai'i, septiembre de 2016) aprobó un nuevo objetivo, por el cual el 30% de cada hábitat marino debe estar incluido en una AMP en el año 2030. Por lo tanto, es necesario realizar un mayor esfuerzo para aumentar las AMPs a nivel mundial y alcanzar los objetivos de conservación.

Los peces depredadores se encuentran en los niveles más altos de las redes tróficas marinas, e incluyen animales como tiburones, meros, pargos, bacalaos, etc. Los peces depredadores, junto con otros grupos animales como mamíferos y aves marinas, se caracterizan por su importancia ecológica, ya que tienen una enorme influencia sobre la estructura y funcionamiento de los ecosistemas marinos. Además, los peces depredadores son recursos económicos muy importantes tanto para la industria pesquera como para el turismo, ya que son el objetivo principal de muchas pesquerías

profesionales y recreativas, además de constituir recursos muy importantes para el buceo recreativo, y por ello muchas especies son consideradas emblemáticas. Tradicionalmente estas especies han sufrido una enorme sobrepesca, lo que ha provocado que en la actualidad muchas especies se encuentren amenazadas por el estado precario de sus poblaciones, e incluso se encuentren agotadas en muchos ecosistemas marinos. Por todo ello, la biomasa y diversidad de peces depredadores es considerada un buen indicador del estado de conservación de los ecosistemas.

Las AMPs han sido identificadas como una herramienta muy eficaz para la conservación y recuperación de las especies de peces depredadores. Sin embargo, el diseño y gestión de las AMPs ha sido objeto de un amplio debate. Aumentar el conocimiento sobre las características de las AMPs que las hacen más eficaces para la protección es crucial para la optimización de los recursos. Los métodos tradicionales de evaluación de las poblaciones de peces depredadores y las medidas de protección pueden presentar sesgos, por lo tanto es esencial identificar el mejor método para la correcta evaluación de sus poblaciones.

Los peces depredadores son un grupo muy valioso que se encuentra con numerosos impactos en el medio, lo cual supone una amenaza para sus poblaciones. Entender los mecanismos ecológicos y sus respuestas a la protección, permiten un diseño mejor de las AMPs para asegurar su correcta conservación. Además, abundan las evidencias de que los planes de conservación basados en especies depredadoras pueden ser implementados para conseguir beneficios más amplios en conservación, ya que existe un nexo entre la presencia de depredadores y los altos niveles de biodiversidad. Por lo tanto, los resultados obtenidos sobre este grupo de especies pueden ser generalizados para conseguir una protección efectiva sobre otros niveles tróficos.

El objetivo de la tesis es evaluar los efectos de la protección sobre las poblaciones de peces depredadores en AMPs, poniendo especial atención en los mecanismos ecológicos, como el efecto de la regulación de la pesca en la abundancia y biomasa de peces, la selección de hábitat y la dinámica temporal de recuperación de las poblaciones de peces. Basándonos en nuestros resultados, el objetivo final es

proponer una serie de medidas que puedan servir de guía para el diseño y gestión de AMPs.

En el **Capítulo 1** se ha evaluado el efecto de la protección sobre la biomasa y densidad de peces depredadores en AMPs localizadas en todo el mundo. Para ello se ha realizado un metaanálisis de datos publicados, en el que se han incluido 29 estudios realizados en 32 AMPs y en los que se evalúan 73 especies de peces piscívoros. Para los análisis se ha aplicado el logaritmo de la razón de respuestas ("log-response ratio"), ponderando los estudios en función de la calidad de su diseño experimental (número de réplicas) y se han incluido variables referentes a las AMPs, como el tamaño de la reserva integral, la presencia o ausencia de la reserva parcial, el tiempo transcurrido desde el inicio de la protección, el grado de vigilancia y el nivel de aislamiento de los hábitats del AMP con respecto a zonas no protegidas. Además, se han evaluado distintos rasgos de vida de las especies, como la talla máxima reportada para la especie, el nivel trófico, el valor comercial, la alimentación, el hábitat, la territorialidad, el comportamiento y la movilidad. Los resultados obtenidos mostraron que, de forma global, hay una respuesta positiva de los peces depredadores en AMPs tanto para su biomasa como para su abundancia. Además, este efecto fue mayor para la biomasa de peces de tamaño medio y la abundancia de especies grandes y con comportamiento gregario. En cuanto a las características de las áreas marinas protegidas, encontramos que el tamaño tuvo un efecto negativo y estadísticamente significativo tanto en biomasa como en abundancia, y que hubo diferencias en función de los distintos niveles de vigilancia, indicando que las reservas pequeñas son efectivas para la recuperación de estas especies siempre y cuando presenten valores elevados de vigilancia.

En el **Capítulo 2** evaluamos la respuesta temporal de la comunidad de peces a la protección a largo plazo en un área marina protegida mediterránea (reserva marina de Cabo de Palos-Islas Hormigas, Murcia, Mediterráneo SO). Además, evaluamos el efecto de la ausencia de vigilancia durante un periodo de tiempo en los patrones de recuperación de las especies. Para ello contamos con una serie de datos de 23 años de censos de peces en la mencionada reserva (es decir, a partir del primer año de su puesta en funcionamiento), y nos centramos en la abundancia y biomasa de toda la

comunidad de peces, de la comunidad de peces excluyendo las especies pelágicas, de los distintos niveles tróficos (considerando los siguientes grupos: piscívoros, mesófagos, micrófagos, omnívoros, herbívoros, planctófagos y detritívoros) y de las especies comerciales que estaban en al menos un 30% de los censos realizados (*Epinephelus marginatus*, *Epinephelus costae*, *Dentex dentex*, *Sciaena umbra*, *Diplodus vulgaris*, *Diplodus sargus*, *Diplodus cervinus* y *Diplodus puntazzo*). Ajustamos las series temporales de datos a varias funciones de crecimiento que tienen significado a nivel ecológico (lineal, exponencial, logística, von Bertalanfy, asintótica, Ricker, Gompertz), y retuvimos la curva que mejor explicaba estadísticamente los datos. Observamos que la biomasa total aumentó mientras que la abundancia disminuyó, tanto para el total de la comunidad como el total sin especies pelágicas. El grupo de los piscívoros fue el único que aumentó hasta alcanzar su capacidad de carga tanto para la abundancia como para la biomasa, mientras que los valores de dichos parámetros para el resto de grupos disminuyeron a lo largo del periodo de estudio. Sin embargo, estos ajustes se hicieron sin tener en cuenta que, tras 15 años de buen funcionamiento, se dio un lapso de varios años en los que la vigilancia disminuyó considerablemente, y con ello decrecieron las abundancias de muchas especies objetivo de la pesca, para después recuperar niveles similares a los iniciales; las curvas ajustadas únicamente al periodo inmediatamente anterior a dicho evento, en el que la vigilancia fue alta y constante en el tiempo, indican un crecimiento exponencial; tras la reanudación de un nivel elevado de vigilancia, los valores de biomasa y densidad de especies depredadoras aumentó de nuevo siguiendo una dinámica exponencial, a un ritmo tal que sugiere que se trata sobre todo de una respuesta de comportamiento de las especies implicadas más que a una respuesta debida al crecimiento poblacional (reclutamiento y crecimiento individual). Todo ello indica que es posible que no se haya alcanzado aún la capacidad de carga real. Las especies comerciales no mostraron patrones iguales frente a la protección a largo plazo, indicando que además del valor comercial otras variables como la mortalidad en el reclutamiento o los ciclos de vida pueden estar explicando los resultados. Además, la reserva marina de Cabo de Palos-Islas Hormigas presentó una biomasa de peces mucho mayor que otras reservas del Mediterráneo, indicando que puede ser una localidad muy importante para la biodiversidad en la zona, y dando

lugar a hipótesis alternativas para explicar estos valores desproporcionadamente altos a escala mediterránea.

En el **Capítulo 3** evaluamos el efecto del método de muestreo en la detección de las respuestas a la protección por peces depredadores, así como el efecto de los distintos niveles de protección ejercidos por 5 AMPs localizadas en el Mediterráneo occidental, ante la posibilidad, detectada en estudios anteriores, de que las técnicas de censos visual aplicadas tradicionalmente no fueran adecuadas para dar cuenta con la suficiente exactitud y precisión de las abundancias de las especies de peces depredadores. Para ello realizamos censos de peces mediante dos metodologías: transectos convencionales (transectos de 50 x 5 m^2; CST por sus siglas en inglés Conventional Strip Transects) y transectos de largo variable georreferenciado combinado con muestreos por distancia (TRT+DS por sus siglas Tracked Roaming Transects combined with Distance Sampling). Además, a partir de los censos TRT+DS pudimos calcular una serie de estimadores de longitud variable pero ancho fijo a 20, 10 y 6 metros (llamados TRT20, TRT10 y TRT6). Se realizó un análisis para cada método o estimador mediante modelos lineares generalizados mixtos incluyendo los factores localidad (cada reserva marina), nivel de protección (integral, parcial, no protegido) y sitio (dando cuenta de la variabilidad espacial aleatoria). Los resultados muestran que los estimadores que cubren mayores áreas por transecto (TRT+DS y TRT20) fueron capaces de detectar un número mayor de especies y proporcionaron estimas más realistas y fiables de los valores de biomasa y abundancia. En cambio, los métodos que cubren áreas menores, y en particular los CST detectaron un número mucho menor de especies y sobreestimaron los valores de biomasa y densidad. En cuando al efecto de la protección, tanto las reservas integrales como las parciales fueron efectivas para la conservación de este grupo de especies, y las reservas de Cabo de Palos y Es Freus mostraron los mayores valores, en contraposición a lo encontrado en Menorca, lo cual puede deberse a una combinación de factores ambientales, como los niveles de producción primaria, y de medidas de gestión, como grado de vigilancia en las reservas.

En el **Capítulo 4** realizamos modelos de distribución de especies en el litoral murciano, considerando las reservas marinas de Cabo de Palos-Islas Hormigas y Cabo

Tiñoso y la zona no protegida de Cabo Cope, para identificar las variables ambientales más importantes para la distribución de especies de peces depredadores (*Epinephelus marginatus*, *Epinephelus costae*, *Mycteroperca rubra*, *Sciaena umbra*, *Dentex dentex*, *Sphyraena viridensis* y *Muraena helena*), así como su proyección espacial, mediante mapas de idoneidad de hábitat. Para identificar diferencias en la selección de hábitats a lo largo del ciclo de vida de las especies, realizamos un análisis para todos los individuos, uno para individuos inmaduros y otro para maduros. Realizamos modelos de solo presencia utilizando el análisis ENFA ("Ecological Niche Factor Analysis"), e incluimos variables derivadas de la batimetría (profundidad, orientación, pendiente, curvaturas, rugosidad), además de una variable sobre el tipo de fondo. Los resultados muestran que las variables relacionadas con la complejidad de hábitat y la profundidad son las que más explicaron la distribución de las especies en todas las zonas, además de la orientación respecto a los vientos dominantes para Cabo Tiñoso y Cabo Cope. Además, encontramos diferencias en la distribución de los individuos en función de su estado de madurez, encontrándose los inmaduros en zonas más someras que los maduros y mostrando mayor sensibilidad a cambios en el hábitat. Todas las zonas mostraron áreas favorables para las especies, indicando que las dos reservas marinas están ubicadas en lugares correctos para su buen funcionamiento. Además, sugerimos la implementación de una nueva reserva marina en la zona de Cabo Cope, pues también cuenta con los hábitats esenciales para las especies.

Los resultados de la tesis doctoral nos permiten ampliar el conocimiento sobre la ecología de los peces depredadores y el efecto de la protección sobre sus poblaciones. Además, la información obtenida nos permite entender de qué forma las AMPs pueden ser más efectivas para la protección de peces depredadores, y por lo tanto elaborar una serie de propuestas de gestión para el correcto establecimiento de nuevas AMPs y gestión de las mismas. En este sentido, sugerimos el establecimiento de redes de AMPs de pequeño tamaño, siempre y cuando se pueda asegurar un elevado nivel de vigilancia en las mismas. Además, proponemos la selección de áreas con una elevada complejidad de hábitat para maximizar los efectos de la protección. Por último, planteamos la necesidad de adoptar métodos de muestreo como el

TRT+DS o TRT20 para poder obtener estimas poblacionales más rigurosas para este grupo de especies.

GENERAL INTRODUCTION

Importance of marine conservation and the establishment of Marine Protected Areas

Marine ecosystems are facing a multitude of anthropogenic disturbances (Halpern *et al.* 2015). Among them, habitat loss is one of the most important impacts on the marine resources (Airoldi & Beck 2007). As a consequence of habitat degradation, structurally complex habitats are becoming rarer (Reise 2005), which has implications in the abundance, richness, diversity, carrying capacity and assemblage stability of marine fauna (Jones *et al.* 2004, Airoldi *et al.* 2008, Calizza *et al.* 2017). Moreover, eutrophication of marine ecosystems is a major problem, which is driven primarily by nitrogen and phosphorus loading (Ngatia *et al.* 2019). In the past few decades eutrophication has increased worldwide (Howarth 2008), leading to reduced water quality, hypoxia and anoxia, algal blooms, alteration of food web structure, habitat degradation and loss of biodiversity (Rabalais *et al.* 2009). Additionally, the introduction of alien species supposes a threat to biodiversity, marine industries and human health (Bax *et al.* 2003). One of the most important vectors transporting alien species is through ballast water of ships that travel between bio-geographic areas for trade and tourism (Bailey 2015). When alien species reach high densities, they may become invasive, dominating the native flora and fauna and displacing native species (Bax *et al.* 2003). Climate change include a number of alterations in ocean productivity (i.e. shifts in temperature, circulation, stratification, nutrient input, oxygen content), with consequences in food web dynamics and a modification in species distributions, hence impacting ecosystems functioning and services in which people, industries and the whole societies depend (Walther *et al.* 2002, Doney *et al.* 2012). Importantly, intensive fishing has been identified as one of the most important threats for marine resources, because of a worldwide overexploitation of fish populations (Lotze *et al.* 2006). Total catches have increased since 1970 for all valuable species groups, and currently 90% of the marine fish stocks worldwide are overexploited or totally depleted (FAO 2018). Moreover, fishing data are not always accurate, and when accounting for all types of fisheries total landings may be much higher than the officially reported to the FAO (Pauly & Zeller 2016). As a consequence, many fish populations are under threat (IUCN 2017), mean size of the species have decreased (Di

Franco *et al.* 2009, Harmelin-Vivien *et al.* 2015) and genetic diversity is reduced in overfished populations (Pinsky & Palumbi 2014). All these impacts suppose important threats to the marine resources and the livelihoods associated. Thus, effective management and conservation actions are necessary for the correct preservation and restoration of the marine resources and the ecosystems (Grafton *et al.* 2010).

Marine Protected Areas (MPAs) are recognized as one of the most effective tools for the conservation of the biodiversity and the fisheries management (Lubchenco & Grorud-Colvert 2015). MPAs consist on the delimitation of an area in which activities, and particularly fishing, are regulated but not necessarily prohibited. There are several terminologies of MPAs depending on their aim and configuration. MPAs may consist in a fully protected or no-take zone, in which all activities are banned; in this case the most common terminology is marine reserve (Pérez-Ruzafa *et al.* 2017). Multiple-use MPAs refer to marine managed zones that include partially protected areas, in which some activities are allowed, such as small-scale fisheries or recreational diving, but strongly regulated. These areas provide a better balance between ecological and social objectives, and are especially important in locations where many livelihoods are linked to the sea, where may be easier to be implemented (Di Franco *et al.* 2016). Partially protected areas are also known as buffer zones when the MPA consists in one or more no-take zones and one or several partially protected areas, generally surrounding the no-take zones. In this case, the most common terminology is MPA (Pérez-Ruzafa *et al.* 2017).

MPAs, and especially no-take zones, are widely recognized as effective areas for the conservation and recovery of fish populations and to dampen the effects of the numerous anthropogenic disturbances. Among the benefits they provide, it is expected an increase in the abundance and biomass of fish to occur (Giakoumi *et al.* 2017, Edgar *et al.* 2014). Because larger fish tend to produce disproportionately more larvae with greater reproductive survival potential, the final consequence is the increase in overall reproductive output in these protected areas (Jennings & Kaiser 1998, Jennings *et al.* 1999, Dulvy *et al.* 2003). Moreover, MPAs are expected to increase the catches in adjacent areas by exporting eggs, larvae or adults, through a process called “spillover” (Harmelin-Vivien *et al.* 2008, Di Lorenzo *et al.* 2016), thus

improving local fishing activities. Additionally, by banning the fishing activity, habitat quality will be improved, what in turn has additional implications for augmenting fish biomass and catch levels (Rodwell *et al.* 2003). MPAs will help to restore ecosystem functioning, such as predation, which mediates energy flows and community assembly within natural systems (Cheng *et al.* 2019). Moreover, it has been demonstrated that MPAs can increase the resilience of coral reef community to disturbances, including coral bleaching, coral diseases, predator outbreaks and storms (Mellin *et al.* 2016). Indeed, MPAs have been proposed as a low-tech, cost-effective adaptation strategy in mitigating climate change effects by promoting carbon sequestration and by buffering against uncertainty in management, environmental variations, and extreme events (Roberts *et al.* 2017). Though, the benefits provided by partially protected areas or buffer zones compared to no-take zones are less clear. They are expected to be less effective than no-take zones (Lester *et al.* 2009), especially when the species that can be harvested are the same that are protected in the no-take zones (Sciberras *et al.* 2013). However, recent studies have found that well-regulated, well-enforced, large and long-established buffer zones can be ecologically effective, especially when they are adjacent to a no-take zone (Zupan *et al.* 2018). Thus, understanding the local effects of buffer zones is essential to determine their effectiveness for the marine resources as well as the local communities.

Currently, there are more than 11 000 designated MPAs worldwide. However, this represents only 4.8% of the world's oceans. Approximately half of that, 2.2%, are highly protected in no-take marine reserves (mpatlas.org 2019). In addition, a good part of the designated MPAs are not yet implemented (Sala *et al.* 2018). Despite the increase in the number of MPAs in the last decades, the proportion of protected areas is insufficient according to the Aichi Biodiversity Target (Convention on Biological Diversity, www.cdb.int). There, at least 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, must be conserved effectively by 2020. More recently, the International Union for the Conservation of Nature World Conservation Congress (Hawai'i September 2016) approved a new global target for MPAs, in which 30 % of each marine habitat must be included in highly protected MPAs and other effective conservation measures by 2030,

in which no extractive activities must be allowed (Sala *et al.* 2018). Thus, despite significant advancements, extra efforts are needed to increase the areas protected worldwide and reach conservation objectives (Grorud-Colvert *et al*. 2019).

Predatory species: importance and conservation

Predatory fish are at the highest levels of the food webs, and include sharks, groupers, snappers, jacks, codfish, etc. When predators are at the top of marine food webs they are known as apex or top predators. These species are considered to have no natural predators in marine ecosystems (Prato *et al.* 2013). Lower level predators, though, are known as mesopredators, and are carnivorous species that are suspected to predation by apex predators. The term predator in this thesis refers to all species occupying the highest levels of marine food webs, i.e equivalent to high-level predatory species. However, the species that are considered apex predators or mesopredators may vary depending on the biogeographic area considered. For example, sharks are widely recognized as apex predators worldwide (Ferretti *et al.* 2010). However, in the Mediterranean Sea, the intense overfishing has led to a shark population decline between 96 and 99.9% (Ferretti *et al.* 2008) and a simplification of communities (Prato *et al.* 2013). In this context, groupers may be considered apex predators in the Mediterraenan Sea, as natural predators are mostly absent.

Predatory fish are characterized by their ecological importance, as they have a strong influence on the structure and functioning of marine communities (Prato *et al.* 2013). Indeed, many of these species act as keystone species in certain ecosystems (Coll & Libralato 2012). There are a number of examples in which predators affect the entire ecosystems through top-down processes, either via direct predation or behaviourally-mediated effects, through resources competition or installing fear in mesopredators (Heithaus *et al.* 2008, Ferretti *et al.* 2010, Newsome *et al.* 2017). For instance, the presence of large top predator species would affect the abundance, growth and behaviour of mesopredator fish, what in turn can increase the recruitment success of other coral-reef fishes, as it was documented in Bahamas with the case of Nassau grouper - *Epinephelus striatus* predating on coney (*Cephalopholis fulva*) and graysby (*Cephalopholis cruentata*) groupers (Stallings 2008). Similarly, the exhaustion

of top predatory species would be followed by the fisheries targeting species at lower trophic levels, which triggers cascade effects, as it was the case of cod (*Gadus morhua*) in Canadian coasts, whose depletion indirectly would have provoked the dramatic increase of sea urchins populations that transformed kelp forests into barrens (Steneck *et al.* 2002). On the other hand, the feeding activity of adult top predators combined with their movements can potentially contribute in a substantial way to nutrient transfer from offshore waters to near-shore reefs (Williams *et al.* 2018). Thus, either direct or indirectly, predatory fish are expected to determine the ecosystem structure and function at different levels.

Predatory fish are important economic resources for both the industry and the tourism. They are the main target of many professional (Pauly *et al.* 1998, Myers & Worm 2003) and recreational fishing (Lloret *et al.* 2008). Additionally, many predatory species are important economic resources for recreational diving (Sala *et al.* 2016), for which many species are considered emblematic, what has an impact on the tourism and the economy in coastal regions. However, the intense overfishing over this group has made many species being currently endangered for the precarious status of their populations (IUCN 2017), and many populations are even depleted in most coastal ecosystems (Sadovy, 2005, Sadovy de Mitcheson *et al.* 2013). Therefore, the biomass and diversity of predatory fish species are good indicators of the conservation status of the entire ecosystems (Barret *et al.* 2018).

MPAs have been identified as useful management tools for the conservation and recovery of high-trophic predators (Micheli *et al.* 2004, Guidetti *et al.* 2014). However, the best design and configuration of MPAs has traditionally been object of debate (Guidetti & Sala 2007, Claudet *et al.* 2008, Edgar *et al.* 2014, Giakoumi *et al.* 2017, Woodcock *et al.* 2017). Understanding the MPA features that maximize their ecological effectiveness is crucial for an optimization of the resources. MPA features such as size, time since the beginning of protection, and levels of enforcement are essential characteristics determining the ecological efficacy of the MPAs (Claudet *et al.* 2008), thus assessing their best design for predatory fish will help to ensure effective protection. Moreover, MPAs need to include the essential habitats for the species, at any life stage, to ensure their effective conservation (Gailaduk *et al.* 2018).

Additionally, to understand the effect of protection on fish populations it is necessary that the sampling methodology is accurate and reports reliable data. However, there are a series of bias associated with sampling methodologies, that can be maximized for the high-level predatory group, thus leading to unrealistic values or erroneous assessments (Ward-Paige *et al.* 2010, Irigoyen *et al.* 2018). Hence, identifying the best sampling methodology is of great interest for a correct evaluation of predatory populations.

Overall, high-level predators are a valuable group that faces numerous threats. Assessing the ecological mechanisms and their responses to protection allow for a better design of MPAs and management of the group. Moreover, it has been evidenced that conservation plans based on apex predators can be implemented to achieve broader biodiversity benefits, as there is a link between predator presence and biodiversity levels (Sergio *et al.* 2006), thus results may be generalizable to achieve conservation over different trophic levels.

Aim of the study

Due to the increasing impacts that marine ecosystems are facing in the last decades, and the special influence that these threats imply on high trophic level species, there is an urgent need to understand the effects of protection on the recovery mechanisms on this group at risk. Moreover, because the establishment of MPAs has not achieved the international conservation targets, there is a call for the establishment of more effective MPAs to ensure the conservation of the marine resources (Sala *et al.* 2018). Increasing knowledge on the ecology of predatory fish and understanding the effects of protection will help to identify the most important features that MPAs must include for the correct conservation and recovery of these species.

The aim of the present thesis is the assessment of the effects of protection on predatory fish in MPAs, with especial emphasis on the ecological mechanisms (i.e. effects of protection on the abundance and biomass, habitat selection, and temporal recovery patterns of the different trophic level groups) underlying the effects.

Moreover, we evaluated different sampling methodologies and their accuracy for the study of predatory fish in MPAs in order to better assess the population status. Finally, based in our results, we propose some management advice to guide the establishment of new MPAs.

The thesis is structured in chapters concerning different perspectives and approaches for assessing the effects of protection on predatory species. In Chapter I we evaluated the effect of protection on the biomass and density of predatory fish in MPAs worldwide distributed through a meta-analytical approach of published data. We specifically evaluated the MPA features that make MPAs ecologically more effective and the fish characteristics that make the species more prone to benefit from protection. In Chapter II we evaluated the temporal population trends of the different trophic levels in the Cabo de Palos-Islas Hormigas MPA, to understand the effects of long-term protection; specific features of this particular MPA, such as having achieved disproportionately high values of fish biomass (even at the global scale), or having suffered a long period of strong poaching pressure (due to a drastic diminution of surveillance) likely preventing the fish assemblage from reaching its carrying capacity, are put in context in order to asses the consequences of an absence in surveillance in the recovery patterns and to better understand the factors that can influence the success of an MPA. In Chapter III we evaluated the effect of protection on the richness, biomass and density of predatory fish in several Mediterranean MPAs. We put emphasis on the effect of the sampling methodology applied in order to get the most accurate and reliable data of this group of species when working in protected and unprotected areas. In addition, we discuss other factores likely responsible for the geographical differences found. In Chapter IV we evaluated habitat selection of predatory fish in the South-Eastern Spanish coast (Region of Murcia) through a species distribution model, to identify the environmental characteristics that determine species occurrence and their spatial distribution in the Cabo de Palos-Islas Hormigas MPA, the Cabo Tiñoso MPA and an unprotected area at the southernmost coast of Murcia. Finally, in the discussion section we combined all the information gathered from the complementary approaches used in the chapters, providing insights for the future design of MPAs to increase their ecological benefits.

CHAPTERS

CHAPTER 1

Factors influencing the effectiveness of Marine Protected Areas for the conservation of predatory fish worldwide

Factors influencing the effectiveness of Marine Protected Areas for the conservation of predatory fish worldwide

1. Introduction

High trophic level teleost fish (grouper, snapper, emperor, codfish, jewfish, etc.) play a crucial role in the functioning of marine ecosystems (Baum & Worm 2009, van Denderen *et al.* 2017), while they are major economic resources for both fisheries and recreational activities (Sala *et al.* 2016). The presence of piscivorous fish species is indicative of the good status of the whole ecosystem (D'agata *et al.* 2016, Valdivia *et al.* 2017, Barrett *et al.* 2018). However, they have traditionally been targeted by the fishing industry (Pauly *et al.* 1998, Myers & Worm 2003), and as a consequence, they are currently depleted in most coastal ecosystems (Jackson 2008, Sadovy de Mitcheson *et al.* 2013). Indeed, many piscivorous species are included in one of the IUCN threat categories (IUCN 2017), such as the endangered *Epinephelus striatus*, *Epinephelus marginatus* or *Petrus rupestris*. Moreover, recent studies have shown that previous estimates on the biomass of highly mobile apex predators were biased, and claim that populations of apex predators are considerably smaller and more precarious than previously thought (Bradley *et al.* 2017, Oken *et al.* 2018).

Marine Protected Areas (MPAs) are usually established for both fisheries management and conservation purposes (Pérez-Ruzafa *et al.* 2017). By banning all kinds of fishing (i.e., no-take zones, hereafter NTZ) and/or implementing strict fishing regulations (i.e., partially protected or buffer zones) they help to replenish fish populations (Giakoumi *et al.* 2017, Sala & Giakoumi *et al.* 2017), improve habitat quality (Rodwell *et al.* 2003), restore ecosystem functioning (Cheng *et al.* 2019) and enhance the exportation of biomass to increase fisheries yields in adjacent areas (Harmelin-Vivien *et al.* 2008). MPAs may consist of only NTZs, known also as marine reserves, or have both NTZs and one or several buffer zones (where certain activities, such as artisanal fishing or recreational diving, are regulated), in which case the most common terminology is MPA (Pérez-Ruzafa *et al.* 2017).

Many studies and previous meta-analyses have attempted to understand how certain MPA features (size, time since the beginning of protection, enforcement, etc.) can influence the effects of protection on marine populations (Halpern & Warner 2002, Côté *et al.* 2001, Micheli *et al.* 2004, Guidetti & Sala 2007, Claudet *et al.* 2008, Edgar *et al.* 2014, Giakoumi *et al.* 2017, Gill *et al.* 2017, Woodcock *et al.* 2017), as well as the biological, commercial and ecological characteristics (commercial value, maximum size, behaviour, etc.) of fish species that result in greater conservation benefits from protection (Mosquera *et al.* 2000, Micheli *et al.* 2004, Claudet *et al.* 2010). As explained below, however, there is still controversy regarding several of these issues.

There is a general consensus that highly enforced MPAs are more effective so that enforcement is found to be a critical variable to achieve conservation benefits (Guidetti *et al.* 2008, McClanahan & Graham 2015, Giakoumi *et al.* 2017, Gill *et al.* 2017). By conservation benefits, we refer to the difference in a conservation outcome (e.g. biomass of fish) when NTZs are compared to unprotected sites; thus, effective MPAs promote ecological restoration inside the MPA by improving conservation outcomes due to the effects of protection. The effectiveness of MPAs appears to increase over time in the long-term (>20 years) (Claudet *et al.* 2008, Molloy *et al.* 2009, Edgar *et al.* 2014, Friedlander *et al.* 2017), although it is likely to slow down as populations reach their carrying capacity (García-Rubies *et al.* 2013). It is noteworthy that large species (Claudet *et al.* 2010), high trophic level species (Micheli *et al.* 2004, Guidetti & Sala 2007) and species with small home range areas (Afonso *et al.* 2016, Abecasis *et al.* 2015, Lee *et al.* 2015) are more likely to benefit from long-term protection. Some studies have even found that biomass and/or abundance can increase in a non-saturating way after more than 20 years (Russ & Alcala 2004, McClanahan *et al.* 2007), highlighting the importance of long-term protection. However, other studies did not find a significant effect of the age of the MPA on the response of fishes to protection (e.g. Côté *et al.* 2001, Halpern & Warner 2002, Tetreault & Ambrose 2007), so no general conclusions can yet be proposed on this issue.

The optimum size of the NTZ has been widely debated. Traditionally, researchers have promoted larger NTZs as being ecologically more beneficial (Claudet *et al.* 2008, 2010, Edgar *et al.* 2014, Friedlander *et al.* 2017), while other analyses found no effect of the size (Côté *et al.* 2001, Halpern 2003, Guidetti & Sala 2007, Lester *et al.* 2009). Furthermore, some studies have proposed an optimum minimum size, such as closures of at least 5 – 10 km^2 to achieve the best conservation potential, in order to avoid the slower recovery trends when sizes are too small (McClanahan & Graham 2015). However, recent studies have found that in the Mediterranean Sea, smaller but well-enforced NTZs are more effective for some commercial species (Giakoumi *et al.* 2017). This has important implications for the design and management of MPA networks, but a more global assessment is still needed to generalize this premise.

In general, it is accepted that buffer (or partially protected) zones are less effective than fully protected areas (Lester *et al.* 2009, Sciberras *et al.* 2013, Giakoumi *et al.* 2017), although they can be effective if properly managed (Hackradt *et al.* 2014). In addition, some studies suggest that latitude may have an effect on protection, with tropical MPAs being more effective than those in temperate zones (Horwood 2000). In a worldwide study of 87 MPAs, conservation benefits were found to be greatest if at least three out of five key features were included, from no-take, old, large, isolated and well-enforced (Edgar *et al.* 2014). Among these features, isolated MPAs would show a more evident effect of protection as habitat discontinuity prevents spillover (Edgar *et al.* 2014).

The potential benefit of MPAs may also depend on the biological, commercial and ecological characteristics of the species (Micheli *et al.* 2004, Claudet *et al.* 2010). Large species are expected to respond better to protection as being more susceptible to fishing mortality (Mosquera *et al.* 2000, Claudet *et al.* 2010). Moreover, commercially important species have been found to benefit the most from protection measures (Mosquera *et al.* 2000, Côté *et al.* 2001, Micheli *et al.* 2004, Tetreault & Ambrosse 2007, Claudet *et al.* 2008, Sciberras *et al.* 2013). Other important characteristics determining species' positive response to protection are related to their habitat and schooling behaviour, so that benthic, solitary or facultative schooling and

non-territorial species would show greater benefits (Claudet *et al.* 2010). Importantly, mobile fish and species with home ranges of any size would profit from protection (Claudet *et al.* 2010; but see Moffitt *et al.* 2009, Abecasis *et al.* 2014). Furthermore, knowledge on how species use space has implications with regard to their potential catchability by fisheries (Jennings & Kaiser 1998, Little *et al.* 2009), as different types of gear are used according to the behaviour of the species, and artisanal and recreational fishery activities decrease with depth (Tyler *et al.* 2009). Responses also vary according to the trophic level of the species. Some studies have found a positive effect on all major trophic groups (Halpern 2003, Soler *et al.* 2015). However, there are a number of studies in which piscivorous fishes show greater responses when compared to other trophic categories. For example, the density and biomass of top predators were 7 and 13 times higher, respectively, inside NTZs when compared to detritivorous fish species in Mediterranean MPAs (Guidetti *et al.* 2014). In addition, in temperate and tropical MPAs, biomass of piscivores increased 60% and density 12%, while values remained almost constant or decreased for other trophic levels (i.e., detritivores, invertebrate feeders, herbivores, omnivores and planktivores; Micheli *et al.* 2004).

Most of the previous meta-analyses focused on the whole fish assemblages (Halpern & Warner 2002, Mosquera *et al.* 2000, Côté *et al.* 2001, Halpern 2003, Claudet *et al.* 2008, 2010) and/or on a few commercially important species (Edgar *et al.* 2014, Giakoumi *et al.* 2017). A few of them, though, addressed the trophic level as a moderator (Micheli *et al.* 2004, Guidetti & Sala 2007, Guidetti *et al.* 2008), indicating that high trophic level species benefitted the most from the protection measures, but without presenting in-depth knowledge on the variables affecting the greater benefits. Those studies did not attempt to identify the MPA features and the biological, commercial and ecological features that affect the responses of the piscivore group to protection, which is of great interest due to the vulnerability of this group to overfishing. Here, by focusing on the piscivore group, we were able to analyse a series of variables regarding the effectiveness of MPAs. Since piscivorous fish species are particularly likely to benefit from the protection offered by MPAs, it is easier to identify the factors affecting the restoration of their populations and to settle controversies regarding which MPA features, among the different available design and management

options, provide the greatest ecological benefits. Furthermore, as this trophic group exhibits a wide variety of biological, commercial and ecological characteristics, it is important to ascertain which features make them more prone to benefit from protection, and this is only possible by limiting the analyses to this group alone.

In this study, we explore the effect of MPAs worldwide on piscivorous fish populations using a meta-analytical approach, which is well-suited when trying to identify a general effect among different studies that individually may have low statistical power (Osenberg *et al.* 1999). The specific aims of the present study were (i) to determine whether and to what extent piscivorous fish benefit from protection worldwide, either in density and/or biomass, (ii) to assess the influence of a series of MPA features on the effectiveness of MPAs in affording better protection of this group of fishes, and (iii) to determine the biological, commercial and ecological characteristics that make piscivorous fish more likely to show a positive response to MPAs. On the basis of the previous literature, we hypothesise that the density and biomass of piscivores will be greater inside NTZs. In addition, we expect older and better-enforced MPAs to afford greater ecological benefits to this group, although larger reserves will not necessarily appear as more effective. Finally, we predict that large species will benefit the most from protection measures. Here, by focusing on the diversity of responses to protection measures within a single trophic group at global scale, we explore patterns that are probably specific to it and that may be different from those previously found for the entire fish community, which is especially important for these commercially valuable populations that are at risk. Our results will help to identify the most important variables influencing the conservation of teleost piscivorous fish species in MPAs worldwide.

2. Methods

2.1. Search for studies and selection criteria

We carried out a bibliographical search on the Web of Science for the period between 1970 and 2016, including the keywords “marine protected area*”, “marine reserve*”

or “no-take zone*”, and refined it with the terms “fish”, “biomass” and/or “densit*”. The aim of the study was to compare data from NTZs (in which all forms of fishing are prohibited) with unprotected areas that were considered as control. However, selected NTZs could belong to MPAs, i.e., with both NTZs and one or several partially protected areas, or to fully protected areas (i.e., with only NTZs). We generally refer to any type of protected area considered in the study as MPAs because this term includes both types.

We identified 448 studies and included 117 additional research articles identified through Google Scholar, using the same keywords for the search. After duplicates were removed, we screened 503 studies. Those that included a comparison of biomass and/or density in NTZs and unprotected areas for any species, and those in which at least one piscivorous fish species was assessed, whatever the aim of the study was (for instance, telemetry studies that might report data for abundance inside and outside NTZs although the main objective was other), were selected for full-text assessment, giving a total of 135 studies selected. These studies were assessed for eligibility providing that they fulfilled the following criteria: mean fish abundance and/or biomass and its error (measured either as standard deviation, standard error, or variance) were reported for at least one piscivorous species inside the NTZ and in unprotected areas for a single MPA, fish were identified at species level, and control areas were in reality open to fishing.

Our search process finally enabled us to include 29 studies performed on 32 MPAs from different biogeographical areas around the world, and involved data on abundance and/or biomass of 73 piscivorous fish species. For studies reporting several years of data for the same MPA, only data for the last year were retained in order to avoid temporal autocorrelation. Data on fish abundance/biomass were generally collected by underwater visual census techniques along transects, although other sampling methods were considered too, such as baited underwater video (BUV).

2.2. Data extraction

From each study, we extracted data on mean biomass and/or density, the error reported (standard deviation, standard error, variance) and sample sizes (i.e., number

of replicate transects or BUV deployments) in NTZs and unprotected areas from the text, tables and figures (in the latter case, using the GetData Graph Digitizer software, available at http://getdata-graph-digitizer.com).

Several characteristics of the MPAs were extracted from the studies in order to examine their potential influence on the effects of protection. MPAs were characterized by the size of the NTZ (measured in hectares); age (i.e., the number of years between the implementation of the reserve and the study date), latitude (in degrees); presence or not of a buffer zone; level of enforcement (according to Guidetti *et al.* 2008) [low ("common illegal fishing and virtually inexistent surveillance"), medium ("illegal fishing occurring but limited by infrequent surveillance"), high ("poaching very occasional if any, patrolling very active and continuous"]; and level of isolation of the protected area in relation to the unprotected area (following Edgar *et al.* 2014) [low (reef habitats reaching the limits of the MPA or even running continuous to fished areas; high connectivity of habitats among the MPA and fished areas), medium (reef habitats surrounded by shallow water < 25 m depth, or small patches of sand; medium connectivity of habitats), high (reef habitats inside MPAs surrounded by deep water > 25 m depth, and/or large expanses of sand; low connectivity among reefs] (see Appendix A for details on MPA features). When some of this information was not available in the study, the corresponding authors were contacted to obtain it.

In addition, for each species, biological (maximum size), commercial (commercial value) and ecological (feeding type, trophic level, habitat, schooling behaviour, territoriality, depth range and mobility) characteristics were compiled from different sources, namely FishBase (Froese & Pauly 2017), IUCN (IUCN, 2017), original research studies (Carpenter & Allen 1989, Shpigel & Fishelson 1991, Heemstra & Randall 1993, Stewart & Jones 2001, Eisenhardt 2003, Floeter *et al.* 2007, Claudet *et al.* 2010, Mellin *et al.* 2016) and expert opinion. Species were categorized according to their maximum size, based on the maximum length reported for the species [small (< 50 cm), medium (51-100 cm), large (> 100 cm)]; commercial value [no value (including species having no or minor commercial value), medium (commercial species with low to medium economic value) and high (commercial species with high to very high economic value)]; feeding type [strict piscivores (those in which more than 90% of

their diet is composed of fish), facultative piscivores (those in which fish are part of the diet but there are other components)]; trophic level [predators (reported values of trophic level between 3 and 3.9), high trophic level predators (values higher than 4.0) (Frisch *et al.* 2014)]; habitat [demersal (including benthic, e.g., grouper), benthopelagic (e.g., barracuda)]; schooling behaviour [gregarious, facultative schooling, solitary]; territoriality [i.e., spatially oriented aggressive behaviour (Börger *et al.* 2008), territorial, non-territorial]; depth range [shallow (< 10 m), medium (10-50 m), deep (> 50 m), broad (any depth)]; and mobility [sedentary (fish that swim less than 50% of the time, e.g., dusky grouper); vagile (fish that swim more than 50% of the time, e.g., jack) (Claudet *et al.* 2010] (see Appendix B for details on the variables for each species).

2.3. Effect size

To quantify the effect of protection on the abundance and biomass of piscivorous fishes, separate meta-analyses were performed for each of the two response variables in order to avoid dependence of data, as in many cases both types of data came from the same study. We used log response ratios as effect sizes (Hedges *et al.* 1999) to quantify the proportional change in density and biomass between the experimental (NTZ) and control (unprotected area) treatments:

$$L_{RR\,ijkl} = Log_e\left(\bar{y}_{NTZ\,ijkl}/\bar{y}_{C\,ijkl}\right)$$

For each log response ratio, its sampling variance was calculated as:

$$V\left(L_{RR\,ijkl}\right) = \frac{SE^2_{NTZ\,ijkl}}{\bar{y}^2_{NTZ\,ijkl}} + \frac{SE^2_{C\,ijkl}}{\bar{y}^2_{C\,ijkl}}$$

with $\bar{y}_{NTZ}$, SE^2_{NTZ} , $\bar{y}_C$ and SE^2_C being the mean and squared standard error of the NTZ and control treatments, respectively, for a response variable, for the combination of *i* studies and *j* MPAs, and *k* moderators and *l* levels in the moderator, for moderator analyses.

For studies in which fish abundance data were only found in the protected area, we assumed that the zeros in the unprotected area were due to a problem of detectability of rare fish species rather than to the complete absence of these species (Emslie *et al.* 2018). In traditional strip transects, detection probability is assumed to

be one, but sampling units are narrow (between 2 and 6 m) and the area covered by the census is usually small, which sheds doubt on the validity of this assumption. The fact that imperfect detectability can lead to biased estimates for the effective monitoring of marine populations has been pointed out by many authors. MacNeil *et al.* (2008) found that the observed individual detectability across almost 50 families ranged from 0.05 to 0.54, highlighting the bias associated with UVC, especially for larger species. Moreover, there is a positive relationship between the probability of detection of a species and its abundance (Dorazio & Royle 2005), so that species exhibiting low abundance and/or patchily distributed are more likely to be undetected (Goetze *et al.* 2017). This situation has led to the intensification of efforts to reduce the risk of false absences, such as increasing the number of observers (Bernard *et al.* 2013), replicates (MacNeil *et al.* 2008), or using sampling methods such as distance sampling and GPS-tracked roaming transects (Irigoyen *et al.* 2018). Thus, in cases where no individual was detected outside the MPA, we added one individual of the species to the total number of replicates in the unprotected area and assigned the same standard error as that reported in the treatment NTZ, in order to increase the variance associated with the effect size estimate, and to give less weight to that study in the whole analysis. This transformation constitutes a novel approach that enabled us to include a greater number of studies in the density response variable. Moreover, this modification of the original dataset did not substantially alter the structure of the data: the modified cases represent 23% of the total; and results for mean abundances at the control sites after the transformation were very low compared to the treatment, with meanNTZ/meanControl ranging from 3 to 861.3 (mean 64.4 ± 22 SE). Tables D1, 2, 3, 4, 5 and 6 in Appendix C show the results of response ratios in the absence of this transformation (i.e., excluding the effect size when no fish data were reported in the control area). When this situation occurred for the biomass, the record was deleted.

2.4. Statistical analysis

Weighted random-effect models were applied to statistically integrate the effect size from the studies. This involved weighting each effect size by its inverse variance, the variance defined as the sum of the sampling variance of the individual effect size and the between-studies variance. With this weighting method, better-designed studies

(because they have a greater number of replicates and lower sampling variance) receive larger weights in the statistical analyses than those with a lower number of replicates (Gurevitch & Hedges 1999). To estimate the heterogeneity among studies, we calculated the Q statistic (Hedges & Olkin 1985) and the I^2 index (Higgins & Thompson 2002). The two indices are complementary and give a better understanding of the total heterogeneity (Higgins & Thompson 2002). High heterogeneity (i.e., a Q statistically significant and $I^2 > 50\%$) implies that effect sizes differ among studies more than might be expected on the basis of sampling error alone, thus there may be moderators explaining part (or all) of it.

First, all species and MPAs were considered together in order to find general responses. Because some MPAs were represented by data derived from more than a single study, mean effect sizes and variances were calculated for the combination of study *i* and MPA *j*. Positive values for response ratios indicated greater density or biomass inside NTZs. Mean effect sizes and 95% confidence intervals were calculated for each response variable. Results were considered to be significantly different from zero when 95% confidence intervals did not overlap zero. Because negative or non-significant results are less likely to be published (Csada *et al.* 1996, Koricheva 2003), Egger's tests (Egger *et al.* 1997), which allow numerical measurement of funnel plots asymmetry by means of a linear regression, were applied for the total data sets in order to identify evidence of publication bias.

In order to explore the effect of both MPA features and fish species characteristics on the response of fish to protection, mixed-effect models were conducted for each of these moderators. Qualitative moderator variables were analysed by means of weighted ANOVAs, and continuous variables by simple meta-regressions. In both cases, a Q_M statistic was calculated to assess the statistical significance of the moderator, as well as a meta-percentage of variance accounted for by the moderator, R^2 (López-López *et al.* 2014). In addition, Q_E statistics were also calculated to assess the model misspecification (i.e., the existence of residual heterogeneity among effect sizes; Koricheva *et al.* 2013; for details on Q_M and Q_E statistics formulas, see Rosenberg 2013). For each moderator, we calculated mean

effect sizes and mean variances for the combination of study *i*, MPA *j*, moderator *k* and category level *l*, to avoid dependence of data.

Finally, we performed multiple meta-regression models including both the statistically ($P \leq 0.05$) and marginally ($P \leq 0.1$) significant moderators in order to find a model that best predicts which MPA features do act as predictors of the effectiveness of their benefits, and which characteristics make piscivores more likely to benefit from protection. We performed Spearman correlation tests and *t*-test comparisons among the variables included in the multiple meta-regressions to find any co-linearity between them.

Size of NTZ was log-transformed, and contrast coding was applied for those moderators with more than two categories (i.e., maximum size, social behaviour, commercial value) to be included in the multiple meta-regressions. All analyses were carried out with the free software R (R Core Team 2015) and the metafor package (Viechtbauer 2010).

3. Results

3.1. General description of MPAs and fish studied

The study included 32 MPAs located in the NE Pacific (4), NW Atlantic (2), Caribbean Sea (1), SW Atlantic (1), SE Atlantic (2), Mediterranean Sea (10), SW Indian (1), SE Indian (2), Coral Sea (3), Java Sea (1), Banda Sea (1) and SW Pacific (4) (Appendix A).

The size of NTZs ranged from 6 to 44 200 ha, with almost 70% occupying less than 1000 ha, and only 10% bigger than 10 000 ha. Original studies stated that unprotected areas and NTZs had a comparable habitat structure and were located at distances that allowed independence between them. Fourteen out of 32 MPAs presented buffer zones, in which artisanal fisheries and different kinds of tourism, such as recreational diving or recreational boat trips, were allowed, and generally surround the NTZs. MPA age ranged from one to 37 years. Most MPAs were highly or moderately enforced, with only 2 MPAs categorised as poorly enforced. Regarding the

isolation levels, most of the MPAs had low isolation (60%); it should be noted that for 4 MPAs information regarding isolation was not available (see Appendix A).

The 73 fish species included in the study belonged to 15 families (Carangidae, Hexagrammidae, Labridae, Lethrinidae, Lutjanidae, Muraenidae, Ophidiidae, Phycidae, Pinguipedidae, Sciaenidae, Scorpaenidae, Sebastidae, Serranidae, Sparidae, Sphyraenidae). The large-sized category included species such as *Epinephelus marginatus* or *Plectropomus leopardus*; medium species such as *Lutjanus apodus* or *Sciaena umbra*; and small species such as *Cephalopholis fulva* or *Serranus* spp. Regarding mobility, sedentary species included all *Cephalopholis* spp., *Epinephelus* spp., and *Sebastes* spp. (among others), and vagile species included most *Mycteroperca* spp., *Lethrinus* spp., *Lutjanus* spp., *Plectropomus* spp., and *Serranus* spp. Our study did not include species belonging to families such as Carcharhinidae, Merlucciidae or Scombridae, characterised in general by being very vagile and having extensive home ranges (although these characteristics vary depending on the species considered), because data for those families were not reported in any of the studies included in our analyses (see Appendix B).

3.2. Overall effect

There was a positive and statistically significant effect of protection on the biomass and density when all MPAs and species were considered together (biomass: log RR = 1.18, 95% CI: 0.58 to 1.80; density: log RR = 1.52, 95% CI: 0.99 to 2.04). However, for both response variables, high values of total heterogeneity among studies indicated that the effect of protection varies among species and MPAs and there must be moderators accounting for that variability (biomass: $Q(20) = 248.73$, $P < 0.0001$, $I^2 = 91.96\%$; density: $Q(43) = 630.07$, $P < 0.0001$, $I^2 = 93.18\%$; degrees of freedom shown in brackets).

Neither Egger's regression test for biomass ($Z = 0.45$, $P = 0.65$) nor for density ($Z = 0.90$, $P = 0.37$) was statistically significant, so there is no evidence of publication bias in the response variables according to this test.

3.3. Influence of MPA features

The level of enforcement exerted a marginally significant effect on the density response variable: highly enforced MPAs positively affected the density of fishes, while poorly enforced ones had a non-significant effect. MPAs enforced at intermediate levels responded positively although to a lesser extent than MPAs with high enforcement (Table 1b). This pattern was similar but, unexpectedly, non-significant for the biomass (Table 1a). For isolation and presence or absence of a buffer zone, all categories in the moderators showed positive but non-significant effects in both density and biomass (Table 1). Latitude had a positive effect on the biomass and density response variables, but it was statistically significant only for density (Table 2). Interestingly, the size of the NTZ was statistically significant and affected negatively the biomass and density of fish, so that the bigger the NTZ, the smaller the effect of protection on both response variables (Table 2). Finally, older MPAs showed a positive but non-significant effect on the response variables (Table 2).

Significant and marginally significant moderators (size of NTZ and latitude for biomass and enforcement, size of NTZ and latitude for density) were included in the multiple meta-regression models. Only two MPAs were characterized by having a low level of enforcement, so we excluded them from these analyses in order to increase statistical power (Hempel *et al.* 2013) and to better discern between the medium and high levels of this moderator.

For biomass, the final model explained 60% of the variance and size of NTZ was the only statistically significant moderator, with a negative effect on the response variable (Table 3a). Similar results were found for density, the model was statistically significant, with the size of NTZ showing a significant negative response to protection (Table 3b). However, enforcement and size of NTZ appeared not to be independent features, so that smaller MPAs were generally better enforced (t-test = 2.29, P = 0.03, geometric mean of NTZ size at high enforcement = 281.84 ha, medium enforcement = 1318.26 ha; Fig. 1A). Moreover, we also found significant differences in enforcement levels at different latitudes, so that enforcement was lower in MPAs situated at lower latitudes (t-test = 4.47, $P < 0.001$, mean latitude at high enforcement = 34.95º, medium

enforcement = 21.55º; Fig. 1B). Finally, Spearman correlation test showed a significant correlation between the size of the NTZ and latitude (r = -0.55, $P < 0.001$). These findings may explain why neither enforcement nor latitude appeared significant in the final model.

Table 1. Results of the weighted ANOVAs for MPA features according to (a) biomass and (b) density, taking categorical moderator variables as predictors.

a) Biomass			95% CI		
Moderator	n	log RR	LB	UB	ANOVA results
Isolation					
High	4	1.45	0.06	2.85	Q_M (2) = 2.91; P = 0.23
Medium	4	0.56	-0.19	1.32	R^2 = 38.52%
Low	11	1.28	0.85	1.72	Q_E (16) = 34.11; $P < 0.0001$
Enforcement					
High	9	1.73	0.78	2.69	Q_M (2) = 3.73; P = 0.15
Medium	10	1.06	0.32	1.78	R^2 = 0.48%
Low	2	-1.06	-2.04	1.57	Q_E (18) = 166.16; $P < 0.0001$
Buffer					
Absence	9	0.86	0.14	1.57	Q_M (1) = 1.10; P = 0.19
Presence	12	1.60	0.74	2.46	R^2 = 1.82%
					Q_E (19) = 232.28; $P < 0.0001$
b) Density					
Isolation					
High	9	1.34	0.31	2.36	Q_M (2) = 0.22; P = 0.90
Medium	7	1.39	0.27	2.52	R^2 = 0%
Low	24	1.59	0.97	2.21	Q_E (37) = 434.67; $P < 0.0001$
Enforcement					
High	29	1.88	1.32	2.45	Q_M (2) = 5.27; P = 0.07
Medium	13	0.95	0.17	1.73	R^2 = 9.30%
Low	2	0.18	-1.88	2.26	Q_E (41) = 612.31; $P < 0.0001$
Buffer					
Absence	25	1.24	0.65	1.85	Q_M (1) = 1.76; P = 0.18
Presence	19	1.89	1.16	2.62	R^2 = 1.39%
					Q_E (42) = 616.42; $P < 0.0001$

n= number of studies. Log RR: effect size 'log response ratio'. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table 2. Results of the simple meta-regressions applied on (a) biomass and (b) density variables for MPA features, taking continuous moderator variables as predictors.

			Model test						
a) Biomass	n	b_j	Q_M	df	*P*	Q_E	df	*P*	R^2
No-take size	21	-1.41	25.10	1	< 0.001	112.80	19	< 0.0001	66.06%
Age	21	0.06	2.20	1	0.11	223.25	19	< 0.0001	12.03%
Latitude	21	0.05	2.66	1	0.10	241.87	19	< 0.0001	4.14%
b) Density									
No-take size	44	-0.89	8.90	1	0.003	422.78	42	< 0.0001	19.87%
Age	44	0.03	0.79	1	0.37	609.41	42	< 0.0001	0%
Latitude	44	0.07	8.20	1	0.004	538.96	42	< 0.0001	19.61%

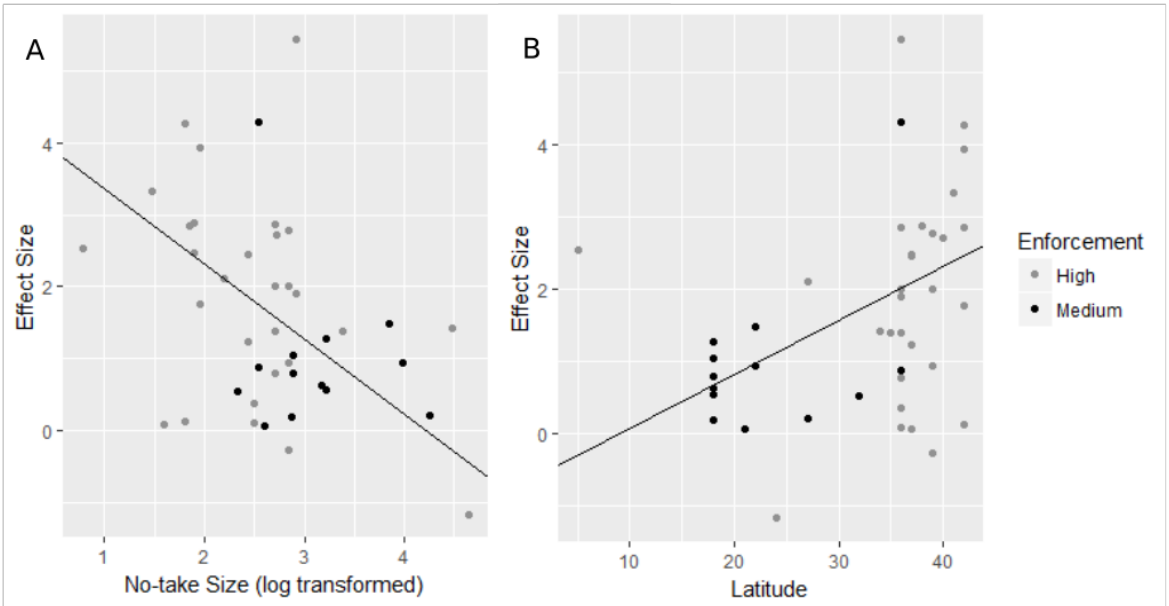
n= number of studies. bj: regression coefficient of each predictor. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. df: degrees of freedom. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table 3. Multiple meta-regression analysis of MPA features for the biomass (a) and density (b) response variables including the marginally and significant moderators.

a) Biomass				
Variable	b_j	SE	Z	*P*
Intercept	4.49	1.40	3.21	0.0013
No- take size	-1.28	0.34	-3.76	0.0002
Latitude	0.02	0.03	0.80	0.42
Full model:	Q_M (2) = 19.71; *P* < 0.0001 R^2 = 60.03% Q_E (16) = 112.49; *P* < 0.0001			
b) Density				
Intercept	2.79	2.04	1.37	0.17
Enforcement	0.44	0.76	0.58	0.57
No-take size	-0.81	0.39	-2.07	0.04
Latitude	0.05	0.03	1.55	0.12
Full model:	Q_M (3) = 12.44 ; *P* = 0.006 R^2 = 33.35% Q_E (37) = 136.77; *P* < 0.0001			

bj: regression coefficient of each predictor. SE: standard error of b_j. Z: statistic for testing the significance of the predictor. p: probability level for the Z statistic. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the full model. Statistically significant moderators are highlighted in bold.

Figure 1. Effect sizes at different enforcement levels for the size of NTZ (A) and latitude (B) moderators.



3.4. Biological, commercial and ecological characteristics responses to fishing protection

The biomass of piscivorous fish responded to protection depending on their maximum size, while no significant response was found for the other fish characteristic moderators considered (Table 4a). Biomass of medium-sized species and, to a lesser extent, of larger ones, exhibited a positive, statistically significant response to protection, while the response of small fish was not significant (Table 4a). Depth category was excluded from the analysis because of the low number of effect sizes of most categories (*n* for depth category broad = 21; deep = 1; medium = 2; shallow = 1).

The response of fish density to protection depended on feeding type, maximum size, commercial value and schooling behaviour of the species (Table 4b). Both facultative and strict piscivorous species showed a positive and significant response to protection, although the effect was greater for the facultative category. Large- and medium-sized species showed similarly greater densities inside NTZs, while for small-sized fishes, the response to protection was non-significant. Commercial species

showed higher density inside than outside NTZs, with a greater effect on high-value commercial species compared to those species with a medium value, while the response of species with no commercial value was non-significant. Regarding schooling behaviour, all three categories showed significant differences between inside and outside NTZs, but this effect was much higher for gregarious and facultative schooling species than for solitary ones (Table 4b).

Table 4. Results of the weighted ANOVAs applied on log RR for the (a) biomass and (b) density response variables for the biological, commercial and ecological fish characteristics.

a) Biomass					
			95% CI		
Variable	n	log RR	LB	UB	ANOVA results
Feeding type					
Facultative	17	1.14	0.48	1.80	Q_M (1) = 0.41; *P* = 0.52;
Strict	10	0.80	0.02	1.60	R^2 = 0
					Q_E (25) = 561.11; *P* < 0.0001
Habitat					
Benthopelagic	4	-0.25	-2.20	1.70	Q_M (1) = 2.13; *P* = 0.14
Demersal	20	1.26	0.65	1.88	R^2 = 4.44%
					Q_E (22) = 262.00; *P* < 0.0001
Maximum size					
Large	16	1.19	0.59	1.79	Q_M (2) = 5.81; *P* = 0.05
Medium	8	1.82	0.89	2.76	R^2 = 13.22%
Small	8	0.40	-0.32	1.14	Q_E (29) = 225.78; *P* < 0.0001
Mobility					
Sedentary	11	1.55	0.60	2.51	Q_M (1) = 0.01; *P* = 0.94
Vagile	19	1.50	0.79	2.22	R^2 = 0
					Q_E (28) = 284.62; *P* < 0.0001
Commercial value					
High	20	1.29	0.83	1.75	Q_M (2) = 2.25; *P* = 0.32
Medium	2	0.68	-0.46	1.83	R^2 = 0
No value	8	0.77	0.16	1.38	Q_E (27) = 133.64; *P* < 0.0001
Schooling behaviour					
Gregarious	5	1.15	-0.06	2.36	Q_M (2) = 0.05; *P* = 0.97
Facultative schooling	5	1.31	-0.05	2.69	R^2 = 0
Solitary	20	1.15	0.52	1.77	Q_E (27) = 278.01; *P* < 0.0001
Territoriality					
Territorial	19	1.32	0.60	2.05	Q_M (1) = 2.29; *P* = 0.13
Non-territorial	6	0.17	-1.13	1.48	R^2 = 1.56%
					Q_E (23) = 282.45; *P* < 0.0001
Trophic level					
Predators	13	1.29	0.59	1.99	Q_M (1) = 0.06; *P* = 0.80
High trophic level predators	20	1.17	0.64	1.71	R^2 = 0

					Q_E (31) = 279.05; P < 0.0001

b) Density

Depth					
Broad	44	1.78	1.30	2.26	Q_M (2) = 2.5; P = 0.28
Deep	6	1.11	-0.30	2.52	R^2 = 2.92%
Medium	12	1.01	0.07	1.94	Q_E (59) = 539.99; P < 0.0001
Feeding type					
Facultative	41	1.72	1.24	2.19	Q_M (1) = 4.59; P = 0.03
Strict	15	0.76	0.02	1.50	R^2 = 7.68%
					Q_E (54) = 783.43; P < 0.0001
Habitat					
Benthopelagic	8	1.07	-0.26	2.40	Q_M (1) = 0.46; P = 0.50
Demersal	44	1.56	1.11	1.99	R^2 = 0
					Q_E (50) = 653.22; P < 0.0001
Maximum size					
Large	36	1.77	1.32	2.22	Q_M (2) = 14.23; P = 0.0008
Medium	21	1.56	0.94	2.20	R^2 = 17.69%
Small	19	0.36	-0.25	0.96	Q_E (73) = 595.69; P < 0.0001
Mobility					
Sedentary	26	1.40	0.79	2.00	Q_M (1) = 0.61; P = 0.43
Vagile	35	1.71	1.19	2.24	R^2 = 0
					Q_E (59) = 667.90; P < 0.0001
Commercial value					
High	42	1.54	1.10	1.99	Q_M (2) = 5.86; P = 0.053
Medium	16	1.04	0.19	1.88	R^2 = 7.14%
No value	19	0.57	-0.10	1.24	Q_E (74) = 612.82; P < 0.0001
Schooling behaviour					
Gregarious	21	2.33	1.63	3.02	Q_M (2) = 7.16; P = 0.028
Facultative schooling	16	1.76	0.87	2.64	R^2 = 10.75%
Solitary	32	1.12	0.55	1.67	Q_E (66) = 1239.27; P < 0.0001
Territoriality					
Territorial	35	1.42	0.88	1.95	Q_M (1) = 0.69; P = 0.41
Non-territorial	22	1.80	1.09	2.50	R^2 = 0.27%
					Q_E (55) = 437.05; p < 0.0001
Trophic level					
Predators	33	1.57	1.05	2.10	Q_M (1) = 0.25; P = 0.62
High trophic level predators	30	1.39	0.84	1.93	R^2 = 0%
					Q_E (61) = 522.90; P < 0.0001

n= number of studies. Log RR: effect size 'log response ratio'. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table 5. Multiple meta-regression analysis of the biological, commercial and ecological fish characteristics for the density response variable including the marginally and statistically significant moderators (i.e., feeding type, maximum size, commercial value and social behaviour).

Density				
Variable	b_j	SE	Z	*P*
Intercept	1.30	0.19	6.70	< 0.0001
Feeding	0.19	0.18	1.08	0.28
MaxTL1	0.59	0.20	2.92	0.0035
MaxTL2	0.28	0.20	1.39	0.17
Commercial1	-0.09	0.19	-0.49	0.63
Commercial2	-0.08	0.21	-0.37	0.71
Social1	0.76	0.23	3.27	0.0011
Social2	-0.11	0.25	-0.44	0.66
Full model:	Q_M (7) = 45.14; *P* < 0.0001			
	R^2 = 32.79%			
	Q_E (113) = 827.52; *P* < 0.0001			

b_j: regression coefficient of each predictor. SE: standard error of b_j. Z: statistic for testing the significance of the predictor. P: probability level for the Z statistic. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the full model. MaxTL1: large fish. MaxTL2: medium fish. Commercial1: high commercial value. Commercial2: medium commercial value. Social1: gregarious. Social2: facultative schooling. Marginally and statistically significant moderators are highlighted in bold.

To perform the multiple meta-regression analysis, we included only those moderators which were significant or marginally significant. In the case of biomass, the only significant moderator was maximum size, so no multiple meta-regressions were performed, and this moderator accounted for 13.22 % of the explained variance. For the density analysis, the moderators included were feeding type, maximum size (transformed into the contrast variables MaxTL1 and MaxTL2, which represents large and medium sizes, respectively), commercial value (transformed into commercial1, including high commercial value, and commercial2 which includes medium commercial value species) and social behaviour (transformed into social1 - gregarious and social2 – facultative schooling species). The full model was statistically significant (Table 5) and explained a high proportion of the variance in the data (32.79%), with the species categories large (MaxTL1) and gregarious (social1) showing a significant positive response to protection. Because the inclusion of contrast variables did not enable us to

understand whether the whole moderator (maximum size and schooling behaviour) were relevant or not in the full model, we performed two additional analyses excluding all variables except the one of interest each time. Thus, once the influence of the other variables was taken into account, both maximum size ($Q_M(2) = 21.09$, $P < 0.0001$; $R^2 = 17.91\%$) and schooling behaviour ($Q_M(2) = 22.03$, $P < 0.0001$, $R^2 = 20.54\%$) were statistically significant in the full model.

4. Discussion

Understanding the MPA features that make piscivorous fishes more likely to benefit from protection is essential for the management of MPAs, because they are a key trophic group in marine ecosystems (Cheng *et al.* 2019), and the first species to be depleted once the ecosystems are altered (Prato *et al.* 2013). Our results only partially corroborated our initial hypotheses. Overall, NTZs harbour higher density and biomass of the studied piscivorous fish species compared to adjacent unprotected areas, as already pointed out by other meta-analyses performed on the whole fish assemblages (Mosquera *et al.* 2000, Côté *et al.* 2001, Halpern & Warner 2002, Halpern 2003, Gill *et al.* 2017) and on piscivorous fishes (Micheli *et al.* 2004, Edgar *et al.* 2014, Giakoumi *et al.* 2017). However, our study goes further by portraying which MPA features and fish characteristics make these species more likely to benefit from protection measures, thus adding insights regarding which are the best MPA design features to achieve conservation objectives for these species.

An important finding of our research, and contrary to what we might expect, was that small NTZs are more beneficial than larger ones to boost biomass and density within the NTZ compared to neighbouring unprotected sites for the set of 73 species (15 families) of piscivorous fish included in the study. This was previously reported in the Mediterranean Sea for the fish density of the whole assemblage and the density of dusky grouper (*E. marginatus*) (Giakoumi *et al.* 2017), and now our results support the generalisation of this assertion at global scale for both density and biomass of the teleost piscivorous trophic group. Traditionally, researchers have advocated larger MPAs to increase their effectiveness (e.g., Halpern 2003, Claudet *et al.* 2008, 2010,

Davies *et al.* 2017), although the implementation of very large MPAs could also entail some disadvantages (Pérez-Ruzafa *et al.* 2017). In fact, an increase in no-take size relative to buffer areas can result in similar values for density and biomass in the two zones and even a negative effect in the NTZs (Sciberras *et al.* 2013). Our study included MPAs with NTZs ranging from 6 (Wakatobi Marine National Park) to 44 200 (Exuma Cays Land and Sea Park) ha. There are several advantages in having a small NTZ, such as ease of enforcement, susceptibility of 'spill-in' - i.e., colonization or migration of commercially targeted species from outside to inside MPAs to be detected more easily (McClanahan *et al.* 2007), or/and protection of species with low mobility, so that the NTZ can embrace their entire home range (Di Franco *et al.* 2018). In fact, small MPAs are expected to protect species with restricted home ranges (Claudet *et al.* 2008, Abecasis *et al.* 2014, 2015), so the minimum size of NTZs will depend on the home range of the species having the highest mobility. In our analysis, we did not include the home range as a moderator (but only mobility) because of a lack of studies for most species and inconsistency in the available estimates in different biogeographical areas. Generally, a positive relationship between body size and home range has been assumed (Kramer & Chapman 1999, Green *et al.* 2015), but recently, Di Franco *et al.* (2018) have found an inverse relationship for a few species in the Mediterranean Sea. For example, our study included large species such as *E. marginatus*, *Plectropomus leopardus*, *Epinephelus costae* or *Pagrus auratus*, with home ranges of around 16.9, 1.9, 2.9 and 13.6 ha, respectively (Zeller 1997, Parsons *et al.* 2003, Afonso *et al.* 2016). These home ranges are smaller than 95% of the NTZs included in the study. So although there is no available information for all species, it is possible that some of the species included in the study do not have large home ranges (as compared to those of most sharks or codfish), which may explain why the studied fish species can benefit from the protection measures offered even by small NTZs.

It has been previously suggested that MPAs would be more effective in tropical zones because the range of fish movements in temperate regions is greater due to wide seasonal variation in water temperatures (Horwood 2000). Moreover, species tend to have longer planktonic larval duration and gene flow in tropical areas (Laurel & Bradbury 2006). However, neither Côté *et al.* (2001) nor Lester *et al.* (2009) found

significant differences in the performance of MPAs in different latitudes, from which they concluded that MPAs would be effective at any latitude. In this respect, our results suggest that there is a weak and marginally significant positive effect of latitude in the effectiveness of NTZs, which actually matches the results of Lester *et al.* (2009) for the density and biomass response variables. However, we found a positive correlation between latitude and enforcement, with NTZs located in higher latitudes having stronger enforcement, which may explain this pattern.

We had expected that older reserves would be ecologically more beneficial. However, we found a positive but non-significant effect of the age of the MPA. Time since the beginning of protection *per se* would be an important variable modulating the effectiveness of MPAs, especially for the piscivorous fishes that are large, have slow growth, long life and late maturity (Jennings *et al.* 1999, Reynolds *et al.* 2005). However, old reserves are more likely to suffer from budgetary restrictions for surveillance at certain times, and thus to trigger periods of poaching (Hogg *et al.* 2017). In fact, in a study performed in 55 MPAs (Bergseth *et al.* 2018), surveys showed that 48% of the fishers living close to them had observed poaching events. Thus, long-term protection alone would not be a good indicator of the ecological effectiveness of MPAs.

We have found a marginally significant effect of the level of enforcement on the density of piscivorous fishes, but, surprisingly, not on biomass. This difference could be due to the lower sample size used for biomass than for density. The novel approach used here by considering that at least one individual was present outside when the species was detected within the MPA (even if zero individuals were censused in the unprotected area) enabled us to include some cases with density data that were not incorporated in the analysis with biomass data. This may have affected the power of the biomass analysis (López-López *et al.* 2014). Enforcement is an essential variable when assessing MPA effectiveness (Guidetti *et al.* 2008, Edgar *et al.* 2014, Giakoumi *et al.* 2017), and effective biodiversity conservation within MPAs worldwide is strongly dependent on human and financial resources (Gill *et al.* 2017). Here, we found a significant relationship between NTZ size and enforcement, with smaller NTZs being better enforced and showing greater effects of protection. Recently, Giakoumi *et al.*

(2017) showed that small and well-enforced Mediterranean MPAs are more effective for the whole fish assemblage and for certain commercially important species. Our results suggest that this is not exclusive to the Mediterranean, so that small and well-enforced reserves may be effective for piscivorous fishes worldwide. This is especially important because the establishment of MPAs is a trade-off between ecological, social and economic factors so that if small MPAs are ecologically effective, they involve less economic effort and social conflict (Giakoumi *et al.* 2017, Pérez-Ruzafa *et al.* 2017).

The presence or not of a buffer zone does not appear to be a significant factor for the success of protection measures with regard to their effect on the density and biomass of the piscivores included in our study. Buffer zones in the MPAs studied were mostly located immediately surrounding NTZs. These partially protected areas are useful tools as multiple-use zones and are especially important with regard to the achievement of local socio-economic benefits (Di Franco *et al.* 2016). These zones are assumed to benefit from spillover from NTZs, either by movements of adults or due to larval dispersion. However, some kinds of fishing are carried out, such as small-scale fishery. If the targets of these fisheries are the same species that are being protected by the NTZs, it is to be expected that buffer zones will not benefit the conservation of these species (Sciberras *et al.* 2013). This result is consistent with the findings that NTZs are generally more effective than partially protected areas in exerting a positive impact on fish assemblages (Lester *et al.* 2009, Sciberras *et al.* 2013, Giakoumi *et al.* 2017, Sala & Giakoumi 2017). In fact, it has been found that large sized buffer zones may even reduce the effectiveness of MPAs (Claudet *et al.* 2008, Sciberras *et al.* 2013), although they can still be very effective if properly designed and managed (Hackradt *et al.* 2014).

Regarding biological, commercial and ecological fish species characteristics, although commercial value has been widely accepted as the major factor driving the response of fish to protection (Mosquera *et al.* 2000, Côté *et al.* 2001, Micheli *et al.* 2004, Tetreault & Ambrose 2007, Claudet *et al.* 2008), examining the studied piscivorous species more closely we found that maximum size and schooling behaviour exert an additional effect. Biomass of medium-sized fish responded best to protection, while large fish, as well as gregarious species, were the groups that responded best in

terms of density. Other studies have found a positive significant response of abundance or biomass to protection with increasing individual fish size (Mosquera *et al.* 2000, Claudet *et al.* 2010, Edgar *et al.* 2014), although this pattern did not appear to be consistent throughout the literature (see Micheli *et al.* 2004), probably because size ranges vary widely across studies. Edgar *et al.* (2014) classified large fish as > 25 cm on the basis of the size of the fishes recorded in the study. In contrast, Mosquera *et al.* (2000) classified fish in seven maximum length classes, from < 10 cm to > 60 cm, and Claudet *et al.* (2010) made three categories, small < 20 cm, medium 20-60 cm and large > 60 cm. Our medium-sized classification is more similar to their large-sized species, so a comparison of these findings is difficult. However, for any classification, which is designed according to the group of species studied in each research project, larger fish tend to benefit more from the effect of protection, either in terms of density (Claudet *et al.* 2010, Edgar *et al.* 2014) or biomass (Mosquera *et al.* 2000, Edgar *et al.* 2014). Maximum size has been proposed as an indicator of the vulnerability of species to fishing pressure because it is related to growth, age at maturity and reproductive output (Jennings & Kaiser 1998, Jennings *et al.* 1999, Dulvy *et al.* 2003), as larger and older fish produce more larvae with greater reproductive survival potential. In fact, commercial and recreational fisheries have always targeted medium- and large-sized individuals (Mellin *et al.* 2016), causing changes in the size structure of the populations.

Schooling fish are well known to be vulnerable to fisheries because schools are easier to target (Dulvy *et al.* 2003). Since the beginning of commercial fisheries, gear and techniques have undergone extensive development with the aim of increasing the captures (Kennelly & Broadhurst 2002), and the improvement of electronic devices and instruments that help locate fish aggregations make schooling species even more vulnerable (Valdemarsen 2001). This may explain why medium- and large-sized species living in schools benefit more from the absence of fishing pressure.

Overall, our results explain part of the total variance in the data, so there may be important moderators that we did not take into account. Moreover, the study has a number of limitations, so results should be taken with caution. Firstly, our study includes only teleost piscivorous fish species, which may rule out generalising our

findings to other predatory species, such as sharks or rays. In fact, MPAs are perceived as only moderately effective for the conservation of sharks and rays, although it may be enhanced for spatially restricted populations, such as some reef shark species (MacKeracher *et al.* 2018).

Moreover, MPAs are typically established in areas where information regarding abundance and/or biomass of fish prior to the establishment of the reserves is lacking (i.e., there is no possibility of performing before-after comparative studies). Thus, the assessment of MPA performance is generally based on a spatial comparison between inside and outside the MPA, and, although individual studies have paid attention to the selection of sampling sites, so that habitats may be comparable, we did not specifically analyse the effect of habitat in our analyses. The effects of protection inside and the influence outside the MPA may depend on (i) the availability of different types of habitats in the two areas, as well as differences in habitat structure (Kramer & Chapman 1999, García-Charton *et al.* 2004), and (ii) the occurrence of differences in habitat quality due to the degrading action of fishing activity (Jennings & Kaiser 1998, Rodwell *et al.* 2003).

In addition, the fishing pressure outside the MPA is likely to determine how species respond to protection (Hopf *et al.* 2016, Pérez-Ruzafa *et al.* 2017), and information regarding fishing intensity and spatial distribution in unprotected areas was lacking. However, in the light of the available data, our research, on the basis of numerous control-impact studies, has enabled us to understand the consistency of the effect of protection under different conditions and offers new general insights on how MPAs enhance teleost piscivorous fish populations worldwide.

In conclusion, our study confirms that both the abundance and biomass of the studied piscivorous fish species benefit from protection measures. MPAs are effective tools to protect piscivores populations even when they are small, but they must be well-enforced to ensure their effectiveness. We thus propose the implementation of networks of small and well-enforced MPAs worldwide in order to provide protection for this key trophic group (Rolim *et al.* 2019). Moreover, as surveillance costs increase exponentially with MPA size, small and well-connected MPAs offer a promising

solution for maximising ecological benefits with limited financial outlay (Pérez-Ruzafa *et al.* 2017). The characteristics maximum size and social behaviour are good indicators of the vulnerability of species to fishing activities, so that medium- and large-sized piscivorous fishes and those living in shoals benefit more from protection. Recent reports (Di Franco *et al.* 2016) highlight the importance of stakeholder engagement and compliance as causal determinants of MPA success, so that besides MPA design attributes, a strong emphasis should be put on studies aiming at providing cues to optimizing MPA governance, i.e., considering not only fishes but also importantly the human component of the management of coastal areas (Hogg *et al.* 2017).

5. Appendices

Appendix A. List of the MPAs included in the analyses and the features that characterise them.

MPA	Latitude	Enforcement	Buffer	Isolation	Age (years)	NTZ size (ha)	Response variable	Reference
Karimunjawa National Park	5°49' - 5°57'	medium	presence	low	0	445	biomass	Yulianto *et al.* 2015
Hoga No take zone (Wakatobi marine national park)	05°12'-06°10'	high	absence	NA	5	6	density	Unsworth *et al.* 2007
Mona Island Natural Reserve	18°05'	medium	presence	low	5	1480	both	Mateos-Molina *et al.* 2014
Keppels	18°19'	medium	absence	low	14	750	both	Evans and Russ 2004
Palm	18°19'	medium	absence	low	14	1660	both	Evans and Russ 2004
Palm	18°19'	medium	absence	low	14	1660	biomass	Graham *et al.* 2003
Palm	18°19'	medium	absence	low	12	1660	both	Williamson *et al.* 2004
Whitsundays	18°19'	medium	absence	low	13	760	both	Evans and Russ 2004
Whitsundays	18°19'	medium	absence	low	13	760	biomass	Graham *et al.* 2003
Whitsundays	18°19'	medium	absence	low	11	760	both	Williamson *et al.* 2004
Admiral Cockburn Land and Sea National Park (ACLSNP)	21°28'	medium	absence	medium	8	400	both	Tupper and Rudd 2002
Mandu Sanctuary Zone	21°39'-23°33'	medium	absence	low	16	7000	density	Fitzpatrick *et al.* 2015
Osprey Sanctuary Zone	21°39'-23°33'	medium	absence	low	16	9500	density	Fitzpatrick *et al.* 2015

Exuma Cays Land and Sea Park (ECLSP)	24°23'	high	absence	NA	11	44200	both	Chiaponne *et al.* 2000
Arvoredo Biological Marine Reserve	27° 35’	medium	absence	high	11	17800	density	Anderson *et al.* 2014
Punta la Restinga Mar de las Calmas	27°36'	high	presence	low	8	155,4	both	Tuya *et al.* 2006
Isla Graciosa e islotes del norte de Lanzarote	28°06'	low	presence	medium	9	7007	both	Tuya *et al.* 2006
San Diego- La Jolla Ecological Reserve	32°51'	medium	absence	medium	31	216	density	Parnell *et al.* 2005
Tsitsikamma Coastal National Park	34°0'	high	absence	high	21	30000	density	Buxton and Smale 1989
Poor Knights Island Marine Reserve	35°29'	high	absence	high	4	2400	density	Denny *et al.* 2004
Hopkins Marine Life Refuge	36°-37°15'	high	absence	low	12	40	density	Paddack and Estes 2000
Big Creek Marine Ecological Reserve	36°07'	high	absence	low	2	309	density	Paddack and Estes 2000
Cape Rodney-Okakari Point Marine Reserve (Leigh)	36°15'	high	absence	low	11	518	density	Cole *et al.* 1990
Cape Rodney-Okakari Point Marine Reserve (Leigh)	36°15'	high	absence	low	23	518	density	Willis and Anderson 2003
Cape Rodney-Okakari Point Marine Reserve (Leigh)	36°15'	high	absence	low	25	518	density	Langlois *et al.* 2005
Cape Rodney-Okakari Point Marine Reserve (Leigh)	36°15'	high	absence	low	25	518	density	Willis and Millar 2005

Tawharanaui	36°22'	medium	absence	low	18	350	density	Langlois *et al.* 2005
Tawharanaui	36°22'	medium	absence	low	18	350	density	Willis and Millar 2005
Pt. Lobos Marine Reserve	36°31'	high	absence	low	23	309	density	Paddack and Estes 2000
Cabo de Gata	36°46'	low	presence	low	1	4653	both	García-Charton *et al.* 2004
Te Whanganui a Hei(Hahei)	36°49'	high	absence	low	10	840	density	Langlois *et al.* 2005
Te Whanganui a Hei(Hahei)	36°49'	high	absence	low	10	840	density	Willis and Millar 2005
Plemmirio	37°00'	high	presence	low	6	80	density	Consoli *et al.* 2013
Cabo de Palos	37°38'	high	presence	high	1	270	both	García-Charton *et al.* 2004
Cabo de Palos	37°38'	high	presence	high	9	270	both	Hacktadt *et al.* 2014
Tabarca	38°10'	high	presence	medium	18	78	both	Hacktadt *et al.* 2014
Cabrera Archipielago National Park	39°09'	high	presence	high	5	696	both	García-Charton *et al.* 2004
Cabrera Archipielago National Park	39°09'	high	presence	high	13	696	both	Hacktadt *et al.* 2014
Cabrera Archipielago National Park	39º09'	high	presence	high	3	696	density	Reñones *et al.* 1999
Cabrera Archipielago National Park	39°09'	high	presence	high	13	696	density	Reñones *et al.* 2012
Tavolara-Punta Coda Cavallo	40°50'	high	presence	medium	1	529	both	Di Franco *et al.* 2009
Miramare	41°37'	high	presence	NA	17	30	density	Guidetti *et al.* 2005
Medes	42°02'	high	presence	medium	21	91	density	Hacktadt *et al.* 2014
Medes	42°02'	high	presence	medium	5	91	density	García-Rubies and Zabala 1990

Scandola	42°21'	high	presence	NA	37	72	both	Harmelin-Vivien *et al.* 2015
Banyuls	42°29'	high	presence	low	25	65	density	Hacktadt *et al.* 2014
Banyuls	42°29'	high	presence	low	1	65	density	Bell 1983

References Appendix A

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Appendix B. List of the species recorded from the studies and their biological, commercial and ecological characteristics.

Species	Feeding type	Trophic level	Maximum size	Medium value	Habitat	Schooling behaviour	Territoriality	Depth	Mobility
Carangoides fulvoguttatus	strict	HTL predator	large	medium	benthopelagic	facultative	non-territorial	broad	vagile
Cephalopholis argus	strict	HTL predator	medium	medium	benthopelagic	gregarious	territorial	medium	sedentary
Cephalopholis cruentata	strict	HTL predator	small	no value	demersal	solitary	territorial	broad	sedentary
Cephalopholis cyanostigma	facult	HTL predator	small	no value	demersal	solitary	territorial	medium	sedentary
Cephalopholis fulva	facultative	HTL predator	small	medium	demersal	solitary	territorial	broad	sedentary
Cephalopholis sexmaculata	facultative	HTL predator	medium	medium	demersal	facultative	territorial	broad	sedentary
Cephalopholis urodeta	facultative	HTL predator	small	medium	demersal	solitary	territorial	medium	sedentary
Cephalophoris spiloparaea	facultative	HTL predator	small	no value	demersal	solitary	territorial	broad	sedentary
Cheilinus trilobatus	facultative	predator	small	no value	demersal	solitary	territorial	medium	vagile
Chrysoblephus cristiceps	facultative	predator	medium	medium	demersal	gregarious	territorial	deep	sedentary
Chrysoblephus laticeps	facultative	HTL predator	medium	medium	demersal	solitary	territorial	broad	sedentary
Dentex dentex	facultative	HTL predator	large	medium	benthopelagic	facultative	non-territorial	broad	vagile
Diplectrum formosum	facultative	HTL predator	small	medium	demersal	solitary	territorial	broad	vagile
Epinephelus caninus	facultative	predator	large	medium	demersal	solitary	territorial	broad	vagile
Epinephelus costae	facultative	predator	large	no value	demersal	solitary	territorial	broad	vagile
Epinephelus fasciatus	facultative	predator	small	medium	demersal	solitary	territorial	broad	sedentary
Epinephelus guttatus	facultative	predator	medium	high	demersal	solitary	territorial	deep	sedentary
Epinephelus leucogrammicus	strict	predator	medium	no value	demersal	solitary	territorial	deep	sedentary
Epinephelus marginatus	facultative	HTL predator	large	high	demersal	solitary	territorial	broad	sedentary
Epinephelus merra	facultative	predator	small	medium	demersal	solitary	territorial	medium	sedentary
Epinephelus morio	facultative	predator	large	medium	demersal	solitary	territorial	broad	sedentary
Epinephelus rivulatus	facultative	predator	small	no value	demersal	solitary	territorial	broad	sedentary
Epinephelus striatus	facultative	HTL predator	large	medium	demersal	solitary	territorial	broad	sedentary
Gnathanodon speciosus	facultative	predator	large	no value	benthopelagic	facultative	non-territorial	broad	vagile
Gomphosus varius	facultative	predator	small	no value	benthopelagic	solitary	territorial	medium	sedentary
Gracila albomarginata	strict	HTL predator	medium	no value	demersal	solitary	NA	broad	vagile
Hexagrammos decagrammus	facultative	predator	medium	no value	demersal	solitary	territorial	medium	sedentary
Hologymnosus annulatus	strict	HTL predator	small	no value	demersal	solitary	non-territorial	medium	vagile
Hyporthodus niveatus	facultative	HTL predator	large	medium	demersal	solitary	territorial	deep	sedentary
Lethrinus atkinsoni	facultative	predator	medium	no value	demersal	facultative	non-territorial	medium	vagile
Lethrinus laticaudis	strict	HTL predator	medium	medium	demersal	gregarious	non-territorial	medium	vagile
Lethrinus nebulosus	facultative	predator	medium	high	demersal	facultative	non-territorial	broad	vagile
Lutjanus apodus	facultative	HTL predator	medium	medium	demersal	gregarious	territorial	medium	vagile

Lutjanus carponotatus	facultative	predator	small	no value	demersal	gregarious	territorial	broad	vagile
Lutjanus mahogoni	facultative	HTL predator	small	medium	demersal	gregarious	non-territorial	broad	vagile
Muraena helena	facultative	HTL predator	large	no value	demersal	solitary	territorial	broad	sedentary
Mycteroperca acutirostris	facultative	predator	medium	no value	demersal	solitary	non-territorial	medium	vagile
Mycteroperca bonaci	strict	HTL predator	large	high	demersal	solitary	territorial	broad	vagile
Mycteroperca fusca	facultative	HTL predator	medium	medium	demersal	solitary	non-territorial	broad	vagile
Mycteroperca insterstitialis	strict	HTL predator	medium	medium	demersal	solitary	non-territorial	broad	vagile
Mycteroperca microlepis	facultative	predator	large	high	demersal	facultative	territorial	deep	sedentary
Mycteroperca rubra	facultative	HTL predator	large	no value	demersal	solitary	territorial	broad	vagile
Mycteroperca tigris	strict	HTL predator	large	medium	demersal	solitary	territorial	medium	sedentary
Mycteroperca venenosa	strict	HTL predator	large	high	demersal	solitary	territorial	broad	vagile
Ophidion elongatus	strict	HTL predator	large	medium	demersal	solitary	territorial	broad	sedentary
Pagrus auratus	facultative	predator	large	medium	demersal	gregarious	non-territorial	broad	vagile
Paralabrax clathratus	facultative	predator	medium	medium	benthopelagic	facultative	non-territorial	medium	vagile
Paralabrax nebulifer	facultative	predator	medium	no value	demersal	facultative	non-territorial	broad	sedentary
Parapercis colias	facultative	predator	small	medium	demersal	facultative	territorial	deep	vagile
Petrus rupestris	facultative	HTL predator	large	no value	demersal	solitary	territorial	broad	vagile
Phycis phycis	facultative	HTL predator	medium	no value	benthopelagic	solitary	territorial	broad	vagile
Plectropomus aerolatus	strict	HTL predator	medium	no value	demersal	solitary	territorial	shallow	vagile
Plectropomus leopardus	strict	HTL predator	large	medium	demersal	solitary	territorial	broad	vagile
Plectropomus oligacanthus	facultative	HTL predator	medium	no value	demersal	solitary	territorial	broad	vagile
Sciaena umbra	facultative	predator	medium	medium	demersal	facultative	territorial	broad	vagile
Scorpaena maderensis	facultative	HTL predator	small	medium	demersal	solitary	territorial	medium	sedentary
Scorpaena porcus	facultative	predator	small	no value	demersal	solitary	territorial	broad	sedentary
Scorpaena scrofa	facultative	HTL predator	medium	medium	demersal	solitary	territorial	broad	sedentary
Scorpaenichtys marmoratus	facultative	predator	medium	medium	demersal	solitary	territorial	broad	sedentary
Sebastes atrovirens	facultative	predator	small	medium	demersal	solitary	territorial	medium	sedentary
Sebastes carnatus	facultative	predator	small	no value	demersal	solitary	territorial	medium	sedentary
Sebastes caurinus	facultative	HTL predator	medium	no value	demersal	solitary	non-territorial	broad	sedentary
Sebastes chrysomelas	facultative	predator	small	medium	demersal	solitary	territorial	medium	sedentary
Sebastes miniatus	facultative	predator	medium	no value	demersal	facultative	territorial	broad	sedentary
Sebastes nebulosus	facultative	predator	small	no value	demersal	solitary	territorial	broad	sedentary
Seriola dumerili	facultative	HTL predator	large	no value	benthopelagic	facultative	non-territorial	broad	vagile
Serranus atricauda	facultative	predator	small	medium	demersal	solitary	territorial	broad	vagile
Serranus baldwini	facultative	predator	small	medium	demersal	gregarious	territorial	broad	vagile
Serranus cabrilla	facultative	predator	small	no value	demersal	solitary	territorial	broad	vagile

Serranus flaviventris	facultative	predator	small	no value	demersal	solitary	territorial	broad	vagile
Serranus scriba	facultative	predator	small	no value	demersal	solitary	territorial	broad	vagile
Sphyraena sphyraena	strict	HTL predator	large	medium	benthopelagic	gregarious	non-territorial	broad	vagile
Sphyraena viridensis	facultative	HTL predator	large	medium	benthopelagic	gregarious	non-territorial	medium	vagile

HLT predator: high trophic level predator

Appendix C. Results of the effect sizes for the density response variable excluding the data for which zero abundance was recorded in unprotected areas.

Table C1. Results of log RR for the density response variable and the total heterogeneity tests.

	Total heterogeneity							95% CI	
	I^2	Q_T	df	P	log RR	SE	Z	P	LB	UB
Density	85.66%	279.04	40	<0.0001	1.027	0.19	5.32	<0.0001	0.65	1.41

I^2 and Q_T: Statistics for testing the heterogeneity among studies. df: degrees of freedom. Log RR: effect size 'log response ratio'. SE: standard error of log RR. Z: statistic for testing the significance of the effect size. P: probability level for the Z statistic. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size.

Table C2. Results of the weighted ANOVAs applied on log RR for the density response variable for the commercial and ecological fish traits.

Density

			95% CI		
Variable	n	log RR	LB	UB	ANOVA results
Depth					
Broad	41	1.09	0.74	1.44	$Q_M(2)=4.82$; p=0.0896
Deep	4	0.56	-0.84	1.96	$R^2=5.02\%$
Medium	11	0.25	-0.43	0.93	$Q_E(53)=297.70$; p<0.0001
Feeding type					
Facultative	39	1.05	0.66	1.44	$Q_M(1)=3.84$; p=0.05
Strict	13	0.32	-0.30	0.94	$R^2=5.15\%$
					$Q_E(50)=458.87$; p<0.0001
Habitat					
Benthopelagic	7	-0.37	-1.42	0.68	$Q_M(1)=6.32$; p=0.011
Demersal	41	1.06	0.68	1.44	$R^2=10.32\%$
					$Q_E(46)=305.7903$; p<0.0001
Maximum size					
Large	30	1.27	0.89	1.67	$Q_M(2)=12.40$; p=0.002
Medium	16	0.86	0.31	1.41	$R^2=18.68\%$
Small	19	0.18	-0.28	0.65	$Q_E(62)=263.80$; p<0.0001
Mobility					
Sedentary	25	0.84	0.33	1.36	$Q_M(1)=2.20$; p=0.138
Vagile	30	1.37	0.90	1.83	$R^2=4.11\%$
					$Q_E(53)=281.99$; p<0.0001
Commercial value					
High	35	1.11	0.73	1.49	$Q_M(2)=7.35$; p=0.025
Medium	13	070	0.03	1.38	$R^2=10.10\%$
Non-commercial	19	0.23	-0.28	0.75	$Q_E(64)=410.50$; p<0.0001
Schooling behaviour					
Gregarious	16	1.41	0.83	1.99	$Q_M(2)=4.61$; p=0.099
Facultative schooling	12	1.20	0.47	1.92	$R^2=8\%$
Solitary	30	0.67	0.24	1.09	$Q_E(55)=322.87$; p<0.0001
Territoriality					
Territorial	33	0.89	0.45	1.34	$Q_M(1)=0.30$; p=0.58
Non-territorial	19	1.10	0.50	1.70	$R^2=0\%$
					$Q_E(50)=324.91$; p<0.0001
Trophic level					
Predators	33	1.08	0.65	1.51	$Q_M(1)=1.21$; p=0.27
Apex predators	28	0.73	0.28	1.19	$R^2=2.32\%$
					$Q_E(59)=338.65$; p<0.0001

n= number of studies. Log RR: effect size 'log response ratio'. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification, that is, the existence of unexplained residual heterogeneity among the effect sizes. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table C3. Multiple meta-regression analysis of commercial and ecological fish traits for density response variable including the marginally and statistically significant moderators (i.e. feeding type, maximum size, commercial value, habitat and social behaviour).

Density				
Variable	b_j	SE	Z	P
Intercept	0.37	0.23	1.58	0.11
Feeding	0.23	0.15	1.46	0.14
MaxTL1	0.64	0.18	3.54	0.0004
MaxTL2	-0.06	0.18	-0.33	0.74
Commercial1	-0.01	0.16	-0.05	0.95
Commercial2	0.03	0.19	0.15	0.88
Habitat	-0.54	0.23	-2.33	0.02
Social1	0.31	0.22	1.41	0.15
Social2	0.24	0.24	1.00	0.31
Full model:	$Q_M(8)= 35.23$; $p<0.0001$			
	$R^2=30.74\%$			
	$Q_E(89)= 397.01$; $p<0.0001$			

b_j: regression coefficient of each predictor. SE: standard error of b_j. Z: statistic for testing the significance of the predictor. P: probability level for the Z statistic. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification, that is, the existence of unexplained residual heterogeneity among the effect sizes. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the full model. MaxTL1: large fish. MaxTL2: medium fish. Commercial1: high commercial value. Commercial2: medium commercial value. Social1: gregarious. Social2: facultative schooling. Marginally and statistically significant moderators are highlighted in bold.

Table C4. Results of the weighted ANOVAs for MPA features according to density, taking categorical moderator variables as predictors.

			95% CI		
Moderator	n	log RR	LB	UB	ANOVA results
Isolation					
High	9	0.30	-0.02	0.62	$Q_M(2)=1.33$; p=0.51
Medium	6	0.07	-0.31	0.45	$R^2=1.23\%$
Low	22	0.44	0.26	0.61	$Q_E(34)=132.14$; p<0.0001
Enforcement					
High	26	1.23	0.75	1.71	$Q_M(2)=4.13$; p=0.127
Medium	13	0.88	0.26	1.50	$R^2=5.67\%$
Low	2	-0.53	-2.22	1.17	$Q_E(38)=252.16$; p<0.0001
Buffer					
Absence	24	0.93	0.43	1.41	$Q_M(1)=0.46$; p=0.5
Presence	17	1.20	0.58	1.82	$R^2=0\%$
					$Q_E(39)=279.03$; p<0.0001

n= number of studies. Log RR: effect size 'log response ratio'. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification, that is, the existence of unexplained residual heterogeneity among the effect sizes. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table C5. Results of the simple meta- regressions applied on density variable for MPA features, taking continuous moderator variables as predictors.

			Model test						
	n	b_j	Q_M	df	p	Q_E	df	p	R^2
No-take size	41	-0.55	5.18	1	0.0228	196.59	39	<0.0001	15.12%
Age	41	0.04	2.91	1	0.0878	268.49	39	<0.0001	4.95%
Latitude	41	0.04	4.50	1	0.033	277.16	39	<0.0001	10.47%

n= number of studies. bj: regression coefficient of each predictor. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. df: degrees of freedom. Q_E: statistic for testing the model misspecification, that is, the existence of unexplained residual heterogeneity among the effect sizes. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table C6. Multiple meta-regression analysis of MPA features for the density response variable including the marginally and significant moderators (no-take size, age and latitude).

a) Density

Variable	b_j	SE	Z	P
Intercept	0.59	1.12	0.53	0.59
No-take size	-0.32	0.26	-1.24	0.22
Latitude	0.03	0.02	1.58	0.11
Age	0.03	0.02	1.34	0.18
Full model:	$Q_M(3)= 8.11$; p=0.043			
	$R^2= 15.69\%$			
	$Q_E(35)= 186.78$; p<0.0001			

bj: regression coefficient of each predictor. SE: standard error of b_j. Z: statistic for testing the significance of the predictor. p: probability level for the Z statistic. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification, that is, the existence of unexplained residual heterogeneity among the effect sizes. Degrees of freedom are shown in brackets. R^2: percentage of variance accounted for by the full model. Statistically significant moderators are highlighted in bold.

CHAPTER 2

Effects of long-term protection on fish populations in the Cabo de Palos-Islas Hormigas Marine Protected Area

Effects of long-term protection on fish populations in the Cabo de Palos-Islas Hormigas Marine Protected Area

1. Introduction

Marine Protected Areas (hereafter MPAs) are spatial management tools for fisheries regulation and biodiversity conservation (Pérez-Ruzafa *et al.* 2017). By banning and/ or limiting the fisheries activity they allow the recovery of the species inside their limits, both in terms of biomass and abundance (Guidetti and Sala 2007, Giakoumi *et al.* 2017). However, protection does not appear to benefit all species in the same way. While some studies suggest that all trophic groups would benefit from protection when compared to unprotected areas (Halpern 2003, Soler *et al.* 2015), it has been widely reported that high trophic groups, that usually include commercially important species, benefit the most from protection measures (e.g. Côté *et al.* 2001, Micheli *et al.* 2004, Guidetti and Sala 2007, Guidetti *et al.* 2008, Claudet *et al.* 2010, Sciberras *et al.* 2013, Guidetti *et al.* 2014, Giakoumi *et al.* 2017, Rojo *et al.* 2019). Therefore, the cessation of fishing pressure within MPAs is likely to affect the trophic structure by facilitating the recovery of high trophic level species and the subsequent cascading effects on prey and basal species (Edgar *et al.* 2017, Cheng *et al.* 2019).

Nevertheless, in addition to human activity, variability in the proportion of the trophic groups in marine communities could be driven by the combined (additive, antagonistic, synergistic or dampened) effect of multiple natural stressors (Boyce *et al.* 2015, Lyman *et al.* 2017, Ruppert *et al.* 2017, Fu *et al.* 2018). Hence, the trophic structure and dynamics of fish assemblages in MPAs may be partially caused by either top-down or bottom-up forces. Bottom-up (or resource-control) forces (i.e. primary producers and preys control the abundance of predators; Stewart and Jones 2001, Hatton *et al.* 2015) are largely driven by oceanographic processes, such as primary productivity, which appears to positively modulate fisheries production in European Seas (Frederikesen *et al.* 2006, Chassot *et al.* 2007, Piroddi *et al.* 2017). For their part, top-down (or consumer-control) forces (i.e. predators controlling the abundance of preys; Baum and Worm 2009, Boaden and Kinsgsford 2015) are difficult to be identified in marine ecosystems because fishing pressure has excessively targeted apex

predators (Pauly *et al.* 1998, Myers and Worm, 2003) and currently most species are virtually absent from coastal ecosystems (Jackson 2008, Sadovy de Mitcheson *et al.* 2013). Consequences of the top-down processes include mesopredator populations to increase due to the lack of apex predators (i.e. "mesopredator release", Ritchie and Johnson 2009) and a decrease in the abundance of preys. Both types of control can be driving major changes in the ecosystems, and the balance between them may depend on the state of the ecosystem, its diversity, the climate fluctuations and the human perturbation that supports (Chassot *et al.* 2007, Baum and Worm 2009, Heath *et al.* 2013). In addition, other factors, including the 'supply-side' influence of settlement and recruitment (Félix-Hackradt *et al.* 2013a, Kimbro *et al.* 2019), and the complexity and heterogeneity of structural habitat (García-Charton *et al.* 2000, 2004), are potentially responsible for the structure and dynamics of fish assemblages.

Long-term protection is necessary to achieve a complete recovery of the populations. There is a number of examples in which time since the beginning of protection appears as an important factor driving ecological effectiveness of MPAs (Guidetti and Sala 2007, Claudet *et al.* 2008, Claudet *et al.* 2010, Giakoumi *et al.* 2017, Edgar *et al.* 2014). Marine studies, however, have the problem of setting historical baselines of ocean abundance, what has led to many efforts done to indirectly estimate pre-exploitation abundances (Fenner 2014, MacNeil *et al.* 2015, Ferretti *et al.* 2018, Leitão *et al.* in press). MPAs are expected to resemble pristine ecosystems (i.e. not affected by anthropogenic disturbance) if adequately established and properly managed (McClanahan *et al.* 2007), with around 50% of fish represented by top predators (Friedlander and DeMartini 2002, Bradley *et al.* 2017). Nevertheless, recent contributions highlight that MPAs may not be able to harbor the same biomass of fish as remote located areas (D'Agata *et al.* 2016, Valdivia *et al.* 2017, McClanahan *et al.* 2019), what hinders the ecological assessments of MPAs. In this situation, most of the studies assessing the effectiveness of MPAs are control-impact studies (i.e. spatial comparison of abundance, biomass or diversity among MPAs and adjacent unprotected areas). However, those kinds of studies do not allow for the assessments of ecological resilience, nor permit to fully understand population change through time, while continuous time series do (Babcock *et al.* 2009). Therefore, any long-term

study aiming at ascertaining the extent of recovery of fish biomass and/or abundance within MPAs after the cessation of fishing activities should establish how near or far the values found are not only from the local carrying capacity (Coll *et al.* 2013, García-Rubies *et al.* 2013, Marra *et al.* 2016), but also the maximum values recorded in the region (Sala *et al.* 2012, Guidetti *et al.* 2014, Giakoumi *et al.* 2017).

On the other hand, the time elapsed since the inception of the protection measures may not be sufficient by itself to explain the dynamics of the communities of fish subject to protection against human activities. Specifically, long-term protection is more likely to suffer from cuts in the budgets at any time and from increases of poaching events (Hogg *et al.* 2017). In fact, high enforcement (i.e. poaching very occasional if any, and patrol very active and continuous, *sensu* Guidetti *et al.* 2008) has been identified as a crucial condition for the correct functioning of MPAs in terms of recovery of the populations (Guidetti *et al.* 2008, Edgar *et al.* 2014, Giakoumi *et al.* 2017, Rojo *et al.* 2019), and has even been found as a critical factor determining the effectiveness of MPAs worldwide (Gill *et al.* 2017).

In this study we analysed the long-term effect of protection on the reef fish community in the Cabo de Palos-Islas Hormigas MPA (SE Spain), which has been protected over 23 years. Specifically, the aims of the study were to evaluate the recovery patterns and to ascertain whether fish biomass and density of (i) the whole fish community, (ii) the different trophic groups and (iii) some commercially important species have reached the carrying capacity of the system. Additionally, because the surveillance was decreased greatly and poaching events became common in the MPA for a few years, (iv) we empirically assessed the shape of the recovery trajectories for different fish species and fish trophic groups under changing enforcement levels. This situation can be considered as a natural experiment, in which the level of enforcement has been manipulated to see how the fish community responds to these changes. Based on the previous literature, we hypothesise that high-level trophic groups will show greater responses and will prompt a top-down control over the other trophic groups; and commercial species will respond positively and similarly to protection. Moreover, we will expect recovery trajectories to reach greater values when the enforcement was high and continuous than for the whole period of study.

2. Material and Methods

2.1. Study area and sampling methodology

The present study was carried out in the Cabo de Palos-Islas Hormigas marine fisheries reserve, an MPA located in the coast of Murcia (SE Spain, SW Mediterranean Sea) (Fig. 1). This marine reserve, which was created in 1995 under fisheries legislation, consists of a no-take zone occupying 270 ha, where all activities are banned, and a partially protected area surrounding the no-take zone and encompassing 1661 ha, where recreational diving and artisanal fisheries are allowed but strongly regulated. The habitat in this MPA consists, in the shallower areas (<16 m deep), of a heterogeneous combination of rocky reefs, patches of sand, and meadows of the seagrass *Posidonia oceanica* that adopt diverse morphological configurations. As a continuation of the mountain range that ends in the peninsula of the cape of Palos, a series of rocky shoals and the small archipelago of Hormigas islands (where the no-take zone is located) are aligned towards the open sea in a northeast direction; in these rocky formations, the infralittoral zone is covered by photophylic algae interspersed with precoralligenous biocoenoses (in the areas more protected from light), and the circalittoral zone is dominated by coralligenous habitats formed mainly by the gorgonians *Paramuricea clavata* and *Eunicella singularis*, until reaching the deepest areas occupied by detritic biocenoses (Calvín *et al.* 1999).

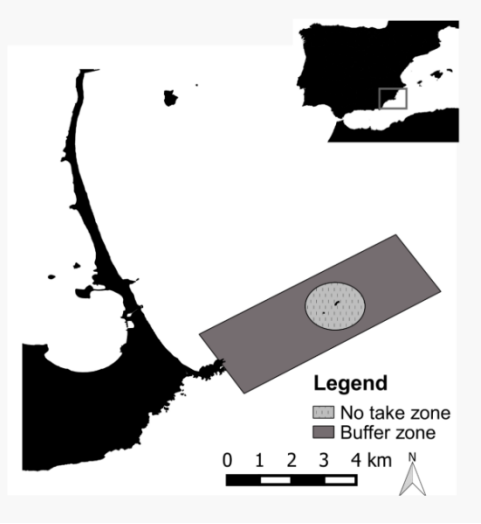


Figure 1. Study area, showing the Cabo de Palos-Islas Hormigas MPA and its location in the SE of Spain, indicating the protection levels.

A monitoring program started in 1996 and it continued until 2018 (except the years 1999, 2001, 2011 and 2012). Although the entire MPA was surveyed each year, only the data issued from the rocky shoals (in the partially protected area) and the Hormigas islands (no-take zone) were taken into account in this study, thus excluding the data taken in the coastal area, because this part is very different (both in terms of habitat structure and human uses), and the effects of protection are much lower than the other parts of the marine reserve. The number of sites and replicates performed in the zones included in the study was variable among years, ranging between 3 and 21 replicates per year (see Appendix A for details on the number of sites and replicates sampled each year). The monitoring was performed through underwater visual censuses (UVC) based in belt transects of 50 x 5 m^2. With this methodology, all fish located in the sampled area were recorded, except small-sized, cryptic species that live associated to the bottom (Harmelin-Vivien *et al.* 1985). For each observation the name of the species was noted and abundance was assigned to one of nine predetermined abundance classes (Harmelin 1987). The size of each individual sighted was visually estimated by considering 2-cm length classes, except for larger fish species, for which 5-cm lenght classes were considered. All UVCs were performed on rocky substrates at depths between 16 and 20 m. UVCs were carried out between 10 and 15 h, when light and water conditions were optimal (see García-Charton *et al.* 2004 for further details on the UVC sampling methodology used). In general, enforcement level (*sensu* Guidetti *et al.* 2008) can be considered as being high during most of the sampling period. However, between the years 2010 and 2014 there were numerous events of poaching and a drastic reduction of the surveillance due to economic constraints.

2.2. Data analysis

2.2.1. Growth curves and model selection

We analysed temporal changes in different descriptors of the reef fish populations (see below). Dates (studied years) were transformed into the variable time, i.e. years since the beginning of protection (year 1995), covering times from 1 to 23.

We selected 7 ecologically meaningful population dynamics models to analyse the recovery trajectories and rates of change in each descriptor (Table 1). Both linear

and exponential models assume that the resources are unlimited. In nature, both growth models can be expressed for a narrow period of time, until there is a limitation of any of the resources. The von Bertalanffy, asymptotic, logistic and Gompertz are all models that approach a carrying capacity at diverse growth rates. Specifically, the logistic and Gompertz are sigmoidal curves, but the logistic is symmetrical while the Gompertz is asymmetrical, thus the asymptotic value is approached more gradually. The Ricker model assumes that there is a peak in the resource, what limits the growth of the populations and forces them to slow down.

These production models were fitted through non-linear curves, applying the nls() function from the stats package (R Core Team 2015). Model selection was based in the AICc (the Akaike's Information Criterion corrected for small sample sizes; Burnham and Anderson 2004). Models with the lowest values of AICc were considered to have better support of the data. When Δ AICc between models was ≤ 2 we considered them to be equivalent in support (Burnham and Anderson 2002). Thus, we additionally calculated the proportion of variation explained by the models using a nonlinear approximation for R^2 (following McClanahan *et al.* 2007):

$$R^2 = 1 - \frac{SS_{reg}}{SS_{tot}},$$

where $\mathrm{SS}_{\mathrm{reg}}$ is the residual sum of squares given the model, and $\mathrm{SS}_{\mathrm{tot}}$ is the total sum of squares in the response. When Δ AICc ≤ 2, for printing purposes we selected the model with the greatest R^2. All analyses were performed in R (R Core Team 2015).

2.2.2. Descriptors evaluated

We carried out separate analyses for the density (abundance · 250 m^{-2}) and biomass response variables, the latter being estimated through the adequate length-weight relationships (expressed in g · 250 m^{-2}). For each response variable, we used total values (considering all species), reduced values (excluding pelagic species) and trophic groups as descriptors. As trophic groups, we included piscivorous fish (species mainly feeding on fish, but also on cephalopods and macroinvertebrates, and scavenger species), piscivorous without *Sphyraena* (same as before excluding the species *Sphyraena* spp. which may distort the results because it forms huge shools aggregated

in certain parts of the rocky shoals and islands, hereafter piscivourous-w*S*), medium-sized invertebrate feeders (species with diets based in medium-sized invertebrates and, at a lesser extent, in small fishes; hereafter medium-IF), small-sized invertebrate feeders (species feeding on small invertebrates, hereafter small-IF), omnivorous fish (species feeding over various trophic levels), herbivorous (species with diets strictly based on primary producers, such as seagrasses or macroalgae), planktivorous (species feeding on zoo- and phytoplankton) and detritivorous fish (species feeding mainly on organic matter accumulated in the sediment) (Bell and Harmelin-Vivien 1983) (Table 2).

Additionally, we selected the most abundant commercial species (i.e. those appearing in at least 30% of the total UVCs), including *Dentex dentex*, *Epinephelus costae*, *Epinephelus marginatus*, *Sciaena umbra*, *Diplodus cervinus*, *Diplodus puntazzo*, *Diplodus sargus* and *Diplodus vulgaris* (Table 2).

We did not separate among levels of protection within the MPA, as previous studies in the area have found that even sedentary species exhibit movements between seamounts and islands (Hackradt 2012). Moreover, the only fishing pressure in the partially protected area comes from small-scale fishing boats which very rarely operate in the marine reserve, and in general fish abundances are not significantly different between the two protected levels (García-Charton *et al.* 2017). Thus, we considered all seamounts and islands to be representative of the habitat and the protected status regardless of the protection level of each one.

Considering the abovementioned increase in poaching activity that occurred in the study area during the period 2010-2014, we carried out three separate analyses: an analysis for the whole studied period (1996- 2018), an analysis that included only the period before the surveillance was cut off and poaching events started to occur (1996-2009), and an analysis for the period in which the surveillance was fully recovered after the interruption (2015-2018). Thus, for each descriptor (total, total reduced, each trophic group and each commercial species) we calculated a global yearly mean and performed the analyses of biomass and density, taking into account

the whole period, the before-interruption and the after-recovery of surveillance periods.

Table 1. Growth population equations used to model temporal trends in fish responses.

Model	Equation	Ecological meaning
Linear	$y = a + m \cdot time$	The linear model assumes constant rates of increase or decrease (m) of the populations from an initial density or biomass (a)
Exponential	$y = a \cdot e^{b \cdot time}$	The exponential model assumes that populations increase or decrease at an exponential rate (b) from an initial density or biomass (a), and the rate is independent of populations size
von Bertalanffy	$y = K(1 - e^{-r\,(time - t0)})$	The von Bertalanffy model assumes a rapid increase (r) that slows down as the population reaches the carrying capacity (K), where t0 is the theoretical time when y = 0
Logistic	$y = \frac{K}{1 + \left(\frac{K - N0}{N0}\right) e^{-r \cdot time}}$	The logistic model assumes that after an initial exponential rate, growth rate (r) gets smaller as the population reaches a carrying capacity (K), where N0 is the initial value for the dependent variable
Asymptotic	$y = K + (N0 - K)e^{-r \cdot time}$	The asymptotic model assumes that the population reaches a carrying capacity (K) at a constant rate (r), where N0 is the initial value for the dependent variable
Gompertz	$y = K \cdot e^{(b \cdot e^{(r \cdot time)})}$	The Gompertz model assumes that growth is slowest at the beginning and at the end of the period (b ; r), and the population approaches the carrying capacity (K) gradually
Ricker	$y = N0 + (a \cdot time)e^{-b \cdot time}$	The Ricker model assumes that the population reaches a maximum peak by an initial rate of increase (a) and decline (b)

Table 2. List of the species found in the study and their trophic position, commercial value and pelagic mobility.

Family	Species	Trophic group	Pelagic	Commercial value
Myliobatidae	*Myliobatis aquila*	medium-IF		commercial
Clupeidae	*Sarda sarda*	PISC	X	commercial
Engraulidae	*Engraulis encrasicolus*	PLAN	X	commercial
Muraenidae	*Muraena helena*	PISC		commercial
Belonidae	*Belone belone*	PISC	X	by-catch
Phycidae	*Phycis phycis*	PISC		commercial
Serranidae	*Anthias anthias*	PLAN	X	no
	Epinephelus costae	PISC		commercial
	Epinephelus marginatus	PISC		commercial
	Epinephelus caninus	PISC		commercial
	Mycteroperca rubra	PISC		commercial
	Serranus atricauda	medium-IF		by-catch
	Serranus cabrilla	medium-IF		by-catch
	Serranus scriba	medium-IF		by-catch
Moronidae	*Dicentrarchus labrax*	PISC		commercial
Apogonidae	*Apogon imberbis*	small-IF		no
Carangidae	*Seriola dumerili*	PISC	X	commercial
	Trachurus spp.	PLAN	X	commercial
	Pseudocaranx dentex	PLAN	X	commercial
Scombridae	*Sarpa salpa*	HERB		by-catch
	Euthynnus aletteratus	PISC	X	commercial
Coryphaenidae	*Coryphaena hippurus*	PISC	X	commercial
Haemulidae	*Pomadasys incisus*	medium-IF		commercial
	Parapristipoma octolineatum	medium-IF		commercial
Sciaenidae	*Sciaena umbra*	PISC		commercial
Mullidae	*Mullus surmuletus*	DETR		commercial
Sparidae	*Boops boops*	PLAN	X	commercial
	Dentex dentex	PISC		commercial
	Diplodus annularis	OMNI		commercial
	Diplodus cervinus	OMNI		commercial
	Diplodus puntazzo	OMNI		commercial
	Diplodus sargus	OMNI		commercial
	Diplodus vulgaris	OMNI		commercial
	Oblada melanura	PLAN	X	commercial
	Pagrus pagrus	OMNI		commercial
	Pagrus auriga	OMNI		commercial
	Sardina pilchardus	PLAN	X	commercial
	Sparus aurata	OMNI		commercial
	Spondyliosoma cantharus	OMNI		commercial
	Spicara smaris	PLAN	X	commercial
	Spicara maena	PLAN	X	by-catch
Pomacentridae	*Chromis chromis*	PLAN	X	no
Labridae	*Coris julis*	small-IF		no

Family	Species	Trophic group	Pelagic	Commercial value
	Labrus merula	small-IF		commercial
	Labrus viridis	small-IF		commercial
	Symphodus dordeleini	small-IF		no
	Symphodus mediterraneus	small-IF		by-catch
	Symphodus melanocercus	small-IF		no
	Symphodus ocellatus	small-IF		no
	Symphodus roissali	small-IF		no
	Symphodus cinereus	small-IF		by-catch
	Symphodus rostratus	small-IF		no
	Symphodus tinca	small-IF		by-catch
	Thalasoma pavo	small-IF		no
Sphyraenidae	*Sphyraena viridensis*	PISC	X	commercial
Mugilidae	*Mugilidae spp.*	DETR	X	commercial
Scorpaenidae	*Scorpaena maderensis*	medium-IF		by-catch
	Scorpaena scrofa	PISC		commercial
	Scorpaena porcus	medium-IF		by-catch
	Scorpaena notata	medium-IF		by-catch
Atherinidae	*Atherina sp.*	PLAN	X	commercial
Molidae	*Mola mola*	PLAN	X	no

PISC: piscivorous fish; medium-IF: medium-sized invertebrate feeders; small-IF: small-sized invertebrate feeders; OMNI: omnivorous species; HERB: herbivorous species; PLAN: planktivorous fish; DETR: detritivorous fish. Commercial species indicate that they are the target of the fisheries, while by-catch indicates that they are occasionally caught but are not the target.

3. Results

3.1. Visually censused reef fish assemblage

During the 23 years of the study period (1996-2018) a total of 62 fish species belonging to 23 families have been observed in the visually censused transects performed in the Cabo de Palos-Islas Hormigas marine fisheries reserve (Table 2). From these, 16 species (25.8%) were piscivorous, 9 species (14.5%) were medium-IF and 13 species (20.9%) were small-IF. For their part, omnivorous represented the 14.5% of the fish assemblage (9 species), while 12 species (19.4%) were planktivorous, 2 (3.2%) species were detritivorous, and only one species (1.6%) - *Sarpa salpa* - has a strict herbivorous diet. Regarding their life habits, 19 species (30.6%) were pelagic, being the rest demersal species. With regard to their commercial value, 39 species (62.9%) have

commercial importance, while 12 species (19.4%) are considered as by-catch (i.e., species of low commercial value subjected to fishing-related mortality, often sold at low price or even as "soup fish"), and 11 species (17.7%) lack such commercial value (Table 2).

3.2. Model selection

Most selected models explaining the temporal change in fish biomass for the whole period of study were logistic or exponential, while, when considering separately the first and last periods of study, exponential models were the ones that best fit the data. In general, models explained a remarkable proportion of the variation in the data (total period R^2 = 41.14% ± 7.63%; first period R^2 = 53.18% ± 8.72%; last period R^2 = 78.83% ± 7.82%; mean values across trophic levels ± SE). In the case of fish density, though, most data fitted Ricker models when accounting for the whole and last periods of study, and linear models for the first period. Again, selected models explained a notable proportion of the variance (total period R^2 = 49.10% ± 6.46%; first period R^2 = 45.15% ± 8.55%; last period R^2 = 60.31% ± 10.37%; mean ± SE). In total, 4 out of the 60 models performed explained less than 10% of the variance in the data. However, for the purpose of the study, which is to show trends in the descriptors, we have kept them even if they are not very informative.

3.2. General responses to long-term protection

Production models showed that, for the whole study period, the fish biomass increased dramatically with time, reaching a carrying capacity of 189 000 g 250 m^{-2} between 10 and 15 years after MPA inception (Fig. 2, Table 3), while the opposite pattern was found for density, for which the variable appeared to decrease with time from 1264 to 741 individuals 250 m^{-2} (Fig. 2). These patterns were consistent both for the total and reduced descriptors (i.e. after extracting the contribution of pelagic species to total values), so that reduced biomass reached a carrying capacity of 142 000 g 250 m^{-2}, and reduced density decreased with time from 317 to 134 individuals 250 m^{-2} (Fig. 2, Table 3).

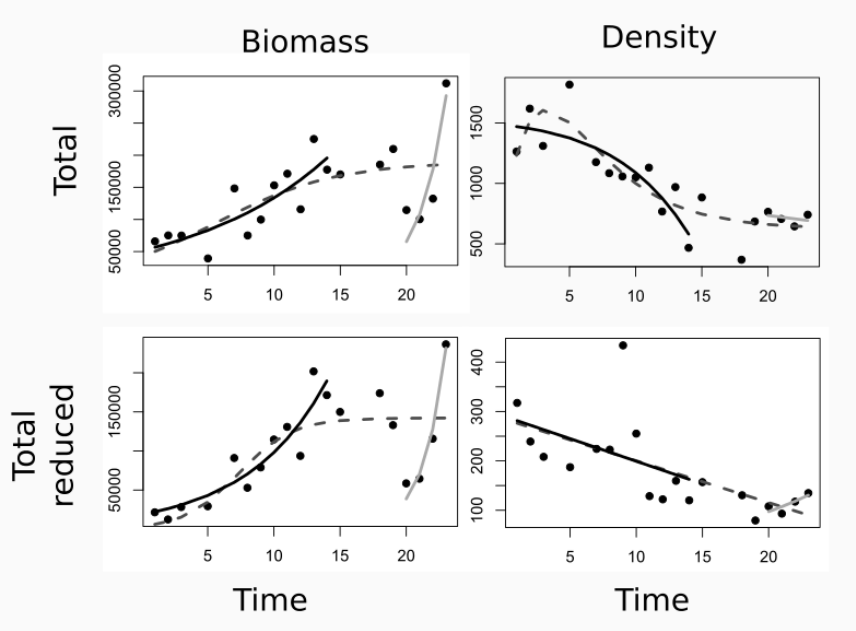


Figure 2. Population trajectories for the descriptors related to the whole community of fish in the Cabo de Palos-Islas Hormigas MPA, for the biomass (expressed as g · 250 m^{-2}) and density (number of individuals · 250 m^{-2}) response variables. The dashed line indicates the model selected when the whole period of study was considered. The black line indicates the population trajectory during the first period in which surveillance was high and constant. The light grey line indicates the trajectory of the fish after the reestablishment of the surveillance.

3.3. Response of trophic groups to long-term protection

Different patterns arose when looking at the temporal trajectory of the biomass of fish trophic groups throughout the whole period of study. Biomass of piscivorous and piscivorous-w*S* fish increased with time following logistic curves, thus reaching a carrying capacity of 163 000 and 138 000 g 250 m^{-2}, respectively (Fig. 3, Table 3). For their part, omnivorous and medium-IF remained almost constant in the period of study around 115 000 and 3 000 g 250 m^{-2}, respectively, although the latter showed a strong increase in the last two years. Biomass of small-IF, herbivorous, planktivorous and detritivorous fish, however, exhibited a population decrease (Fig. 3).

Table 3. Carrying capacity values obtained for the biomass (g · 250 m^{-2}) and density (abundance · 250 m^{-2}) variables through the logistic models for the whole period of study and those calculated from the initial exponential trend during the first period.

Variable	Descriptor	Carrying capacity from the whole period of study	Carrying capacity from the initial exponential function
Biomass	Piscivores	$16.28 \cdot 10^4$	$54.52 \cdot 10^5$
Biomass	Piscivores-w*S*	$13.77 \cdot 10^4$	$22.34 \cdot 10^6$
Biomass	Total	$18.94 \cdot 10^4$	$12.34 \cdot 10^6$
Biomass	Total reduced	$14.22 \cdot 10^4$	$36.09 \cdot 10^6$
Biomass	*D. dentex*	$14.14 \cdot 10^3$	$22.81 \cdot 10^5$
Biomass	*E. marginatus*	$78.15 \cdot 10^3$	$14.23 \cdot 10^6$
Biomass	*D. cervinus*	$12.69 \cdot 10^2$	$33.35 \cdot 10^4$
Density	Piscivores-w*S*	24.34	$37.62 \cdot 10^2$
Density	*E. marginatus*	9.27	$27.38 \cdot 10^2$

In the case of fish density, all trophic groups analysed, except piscivorous, piscivorous-w*S* and medium-IF, showed a decrease in observed numbers (Fig. 3). In the case of piscivorous fish, their density decreased at the beginning of the period, and then showed a slight increase at the end. For their part, both piscivorous-w*S* and medium-IF showed a remarkable increase in their populations, reaching a carrying capacity of 24.3 individuals 250 m^{-2} (in the case of piscivorous-w*S*, Table 3) or a peak of about 12.5 individuals 250 m^{-2} after 11 years of protection and a subsequent decrease (in the case of medium-IF) (Fig. 3). The fact that density of piscivorous fish did not follow the same pattern than piscivorous-w*S* highlights the variability that *Sphyraena* spp. adds to the group (Fig. 3).

3.4. Response of commercial species to long-term protection

Patterns were not consistent among commercial species when considering the whole study period. The species *D. dentex*, *E. costae*, *E. marginatus*, *S. umbra* and *D. cervinus* showed an increased both in terms of biomass and density (Fig. 4). Moreover, except the biomass of *E. costae*, that increased linearly, and of *S. umbra*, that remained mostly constant until the last years, in which it increased exponentially, density and biomass of the other species reached a carrying capacity between 5 and 10 years after the implementation of the protection measures. For their part, the density of *D. puntazzo*, *D. sargus* and *D. vulgaris* and the biomass of *D. vulgaris* showed a decrease

in their populations, while the biomass of *D. puntazzo* and *D. sargus* remained constant, the latter increasing in the last year (Fig. 4).

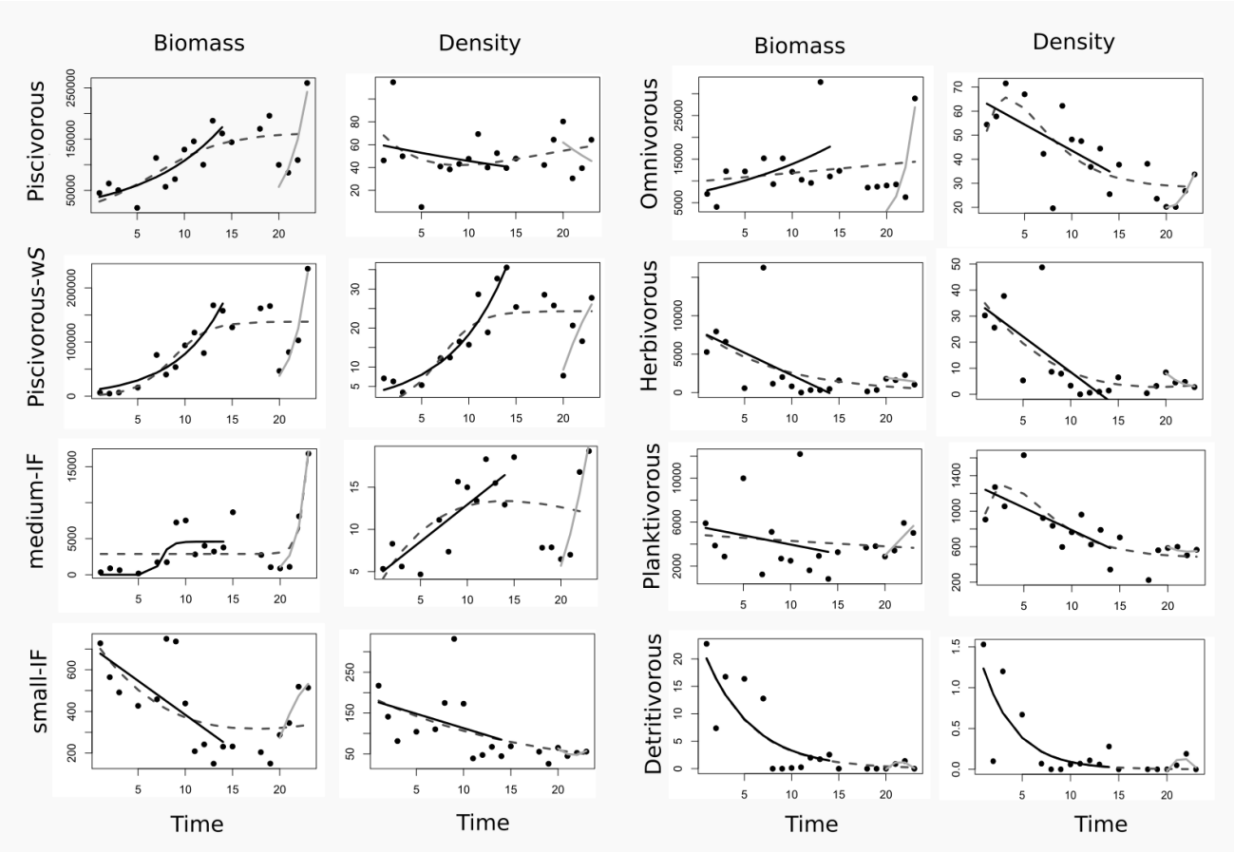


Figure 3. Population trajectories for the trophic descriptors in the Cabo de Palos-Islas Hormigas MPA, for the biomass (expressed as g 250 m^{-2}) and density (individuals 250 m^{-2}) response variables. The dashed line indicates the model selected when the whole period of study was considered. The black line indicates the population trajectory during the first period in which surveillance was high and constant. The light grey line indicates the trajectory of the fish after the reestablishment of the surveillance.

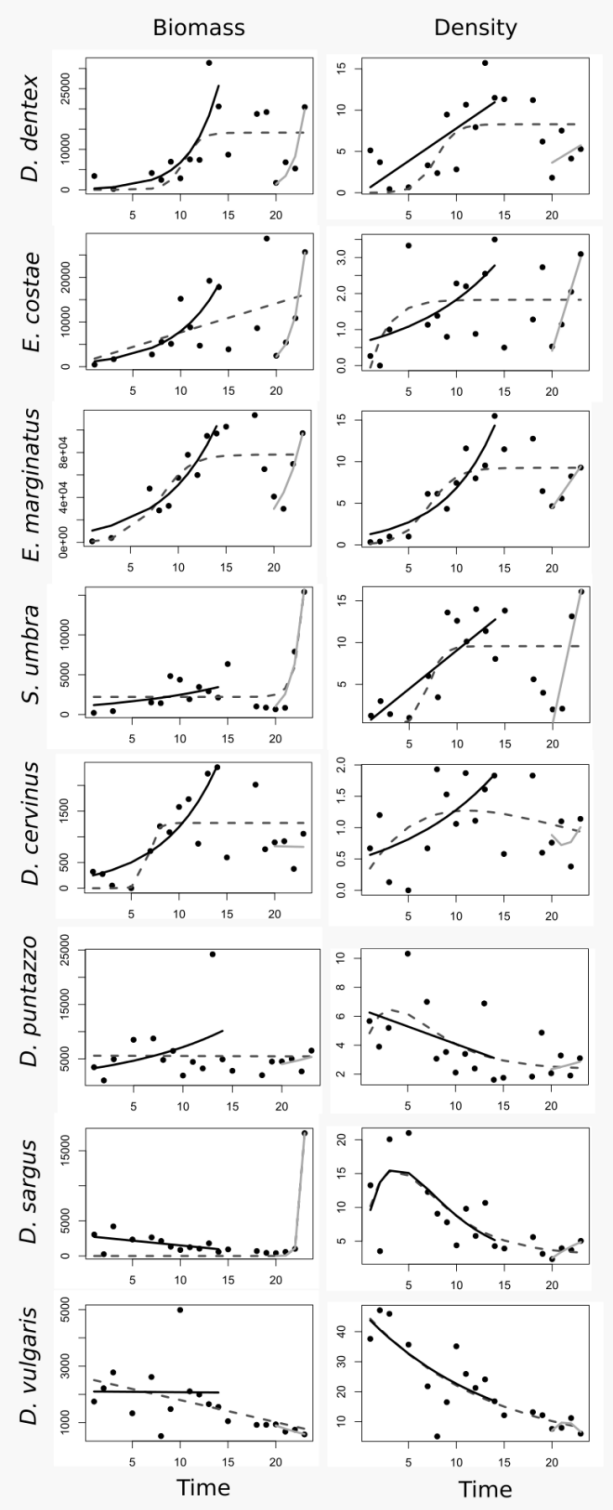


Figure 4. Population trajectories for the commercial species in the Cabo de Palos-Islas Hormigas MPA, for the biomass (expressed as g · 250 m^{-2}) and density (number of individuals · 250 m^{-2}) response variables. The dashed line indicates the model selected when the whole period of study was considered. The black line indicates the population trajectory during the first period in which surveillance was high and constant. The light grey line indicates the trajectory of the fish after the reestablishment of the surveillance.

3.5. Effect of reduced surveillance

During the 2010-2014 period, as a likely result of the drastic reduction in surveillance at that time, in general, the values of density and biomass dropped noticeably (Fig. 1-3). When we fit the population growth models separately for the periods immediately before and after this dysfunctional period, for most descriptors that showed an increase throughout the whole period (density and/or biomass of the whole assemblage, trophic groups and commercial categories), whatever the model selected, populations growth was generally much higher during the first period of the study (when surveillance remained high), fitting either to linear or exponential functions (Fig. 1-3). Because logistic functions imply an initial exponential increase, for those descriptors in which total periods fitted a logistic model and the first period fitted an exponential function we calculated new carrying capacities based on the exponential trend of the first period: overall, the estimated values were 1 to 3 orders of magnitude greater than the ones estimated by considering data for the whole study period (Table 3). In the same way, the last period (after the full recovery of the surveillance activities) showed in general exponential and linear increases for most of the descriptors studied (Fig. 1-3). Although these last models were fitted to data belonging to 4 years only, the recovery after the reestablishment of surveillance is remarkable, requiring less time to reach values practically equivalent to what previously required more than a decade.

4. Discussion

Evaluating long-term effects of protection on reef fish populations is essential to understand the ecological mechanisms occurring in MPAs (Babcock *et al.* 2009). Moreover, this information is necessary to keep effective protection over a minimum number of years to achieve full conservations benefits (Gill *et al.* 2017). Here, we evaluated the responses to protection of the reef fish assemblage as a whole, of fish species grouped in trophic levels, and of some selected commercially important species taken individually, both in terms of density and biomass, in an ecologically effective temperate MPA 23 years after its declaration. Moreover, we explored

whether a prolonged episode of poaching has been able to affect the possibility to reach or not such a carrying capacity; in addition, we discuss whether the values of biomass and density obtained locally differ, and in that case, how much, from the maximum values recorded at the regional (Mediterranean) scale.

Reserve effect on the whole fish assemblage

Our results show that fish biomass increased dramatically after the inception of the protection measures in the Cabo de Palos-Islas Hormigas marine fishery reserve. This pattern is likely to be primarily due to the existence of a strong fishing pressure in the area prior to the declaration of this MPA (Micheli *et al.* 2004), a situation corroborated by the testimony of artisanal fishermen operating in the area, who in addition report very low fishing catch at that time. Noticeably, the patterns shown by the density of the whole fish assemblage differed from what experienced by its biomass, so that the former decreased while the latter increased throughout the study period. This can be due to the fact that protection measures promote the establishment of fewer individuals residing in the area, but with larger sizes (i.e. older fish). When species have long lives and attain large sizes, there is a greater difference between the sizes of juveniles and adults than in the case of smaller species. Higher positions in food webs make this phenomenon more evident, as piscivores have longer lives and larger sizes than species of lower trophic levels (Dunic & Baum 2017). Thus, the differences in growth patterns may be responsible for the differences found between biomass and density trends.

In our study, considering the whole study period, the time required to achieve the carrying capacity of the whole community ranged from 10 to 15 years depending on whether or not pelagic species were included in the analysis. These times are longer than those found for responses of the reef fish community in other Mediterranean MPAs, such as the Es Freus and Palma MPAs (5 years; Coll *et al.* 2012), but are comparable to MPAs located elsewhere (10-20 years; McClanahan *et al.* 2007, Babcock *et al.* 2009, McClanahan *et al.* 2016). The question of how many years are expected to elapse until the magnitude of the results of protection measures reach their maximum magnitude is not trivial, since it influences the expectations raised among potential

users of the MPA. Some studies linked the velocity of the response of fish species to protection to the size of their home range, so that if target species have a small home range and exhibit high site fidelity, their abundance may increase significantly as early as 3-4 years since the inception of protection measures (Abecasis *et al*. 2015). As our data show, however, the home range does not predict how much the abundance or biomass of that species can increase in the long term, as other factors are potentially responsible for the magnitude of this increase, especially in the case of long-lived species (see below).

Reserve effect on the trophic structure of the fish assemblage

When focusing on the trophic levels, we found that piscivorous fish and, to a lesser extent, medium-IF, were the only groups increasing in abundance and biomass throughout the whole study period, while the others remained constant or decreased, depending on the response variable under scrutiny. This is in accordance with previous studies which found higher abundance of high trophic-level species compared to other trophic groups in MPAs (Mosquera *et al.* 2000, Côté *et al.* 2001, Micheli *et al.* 2004, Guidetti and Sala 2007, Guidetti *et al.* 2008, Claudet *et al.* 2010, Guidetti *et al.* 2014, Giakoumi *et al.* 2017). This positive effect might be mainly due to individual growth of adults, since protection reduces fishing mortality. This pattern has been widely reported in the Mediterranean (e.g. Guidetti and Sala 2007, Giakoumi *et al.* 2017) and elsewhere (Mosquera *et al.* 2000, Halpern 2003) and is especially important for high trophic groups and large-sized species that have traditionally been exploited by both commercial and recreational fisheries (Pauly *et al.* 1998, Mellin *et al.* 2016).

Moreover, the increase in abundance and body size is related to greater reproduction capacities, as larger and older individuals produce disproportionately more larvae with greater survival potential (Jennings and Kaiser 1998, Jennings *et al.* 1999, Dulvy *et al.* 2003, Marshall *et al.* 2019). Although larval dispersal can reach hundreds of kilometers (Di Franco *et al.* 2015), it has been found that self-recruitment is more common than previously thought and can take place even in small MPAs (Berumen *et al.* 2012). This seems actually to be the case of the Cabo de Palos-Islas Hormigas marine reserve: larval dispersal simulations of *E. marginatus* revealed that it

is probably one of the MPAs with a higher self-recruitment rate in the entire south-western Mediterranean Sea for this emblematic species (Orenes *et al.* in prep.). This, coupled with the protection of the habitats, may have led to an increase in the recruitment of individuals in the MPA. Additionally, the enhancement in habitat quality can be partially responsible of spill-in processes, in which mobile species migrate and colonize MPAs as a response to fishery disturbance outside and better conditions inside (McClanahan *et al.* 2007, Eggleson and Parsons 2008).

The fact that piscivorous and medium-IF fish increased over the period of study while other trophic groups remained constant or decreased can be attributed in part to the occurrence of top-down processes (Boaden and Kinsgsford 2015). Other long-term studies found trends to increase the abundance/biomass of different trophic groups, such as herbivores and invertebrate eaters, while some families displayed differing trends, suggesting that control made by predators may be species and site specific (McClanahan *et al.* 2007). Top-down processes have been documented for predatory fish preying on invertebrates in the Mediterranean Sea (Micheli *et al.* 2005, Guidetti 2006) and elsewhere (Shears and Babcock 2002, Babcock *et al.* 2009). Moreover, indirect mechanisms such as behaviorally-mediated effects have been proposed, in which changes in the abundance of a species results in a modification in the behaviour of a second species (i.e. risk effect) that finally influences a third species (*sensu* Heithaus *et al.* 2008). Though, in our study area, in which fishing is prohibited or very regulated, and the decrease in abundance and biomass has occurred over several trophic groups, the most probable explanation is the top-down control by an increase in the high trophic groups, either directly or indirectly.

Reserve effect on selected commercial fish species

Although we had expected all commercial species to show similar long-term responses to protection, as was the case, for instance, in the Medes Islands MPA (García-Rubies *et al.* 2013), we found that only some commercial species showed an increase in their abundance and biomass over time (*E. marginatus*, *E. costae*, *D. dentex*, *S. umbra* and *D. cervinus*) while other commercial species declined (*D. sargus*, *D. puntazzo* and *D. vulgaris*), indicating that commercial value alone does not explain the observed

patterns. All these species have in common to present high commercial value, but they differ in their biological and ecological features. Firstly, *E. marginatus*, *E. costae*, *D. dentex* and *S. umbra* belong to the piscivorous group, while *D. cervinus*, *D. sargus*, *D. puntazzo* and *D. vulgaris* are omnivorous species. The fact that the piscivores have increased more intensively may be due to the lack of natural predators in the area (Prato *et al.* 2013). Moreover, *D. sargus*, *D. puntazzo* and *D. vulgaris* have been found to be very sensible in their larval stage, with high mortality rates immediately after settlement, probably due to predation by cnidarians, cephalopods and several fish species (Macpherson *et al.* 1997), what may explain their lack of recovery in the area. In fact, it was found that abundance of recruits of *D. sargus*, *D. puntazzo* and *D. vulgaris* in the study area was directly related to abundance of settlers, indicating that mortality of recruits was more relevant for their population structure, while no relationship was found for *D. cervinus* (Félix-Hackradt *et al.* 2013a).

Fish carrying capacity and poaching

MPAs promote the recovery of the populations that live within their limits, provided that they are protected for long enough (MacNeil *et al.* 2015), and that enforcement is high and constant through time (Guidetti *et al.* 2008, Giakoumi *et al.* 2017). As mentioned above, our results show that piscivores have reached their carrying capacities between 10 and 15 years, a period of time comparable to other studies performed in the Mediterranean Sea (García-Rubies *et al.* 2013). However, when we fit the temporal trajectories differentiating between periods of high enforcement before and after the period when enforcement fell in quality, we observe that during the first 14-years period the population growth was clearly exponential, showing no signs of approaching an asymptote (see also García-Charton *et al.* 2008); under these circumstances, the estimated carrying capacity would be 1 to 3 orders of magnitude greater than that calculated for the entire study period. Other MPAs have shown continuous increases in their populations after decadal times of protection; for instance, in the Port-Cros National Park, which was established in 1963 and has had effective enforcement since the beginning, dusky grouper (*E. marginatus*) populations are still increasing in terms of biomass after 55 years of protection (Astruch *et al.* 2018). Similarly, a study performed in 2 MPAs in the central Philippines showed that

biomass of predatory fish after 9 and 18 years fitted exponential models, and the carrying capacity estimated from the data gave unrealistically high values (Russ and Alcala 2004). However, in the absence of baselines, it is difficult to ascertain how unrealistic those measurements are. It is absolutely necessary to continue the long-term monitoring efforts in order to check how long the fish biomass can continue to grow in this marine reserve.

Fish biomass recovery after recuperating high enforcement level

The last 4-years period showed a rapid increase of many descriptors of the fish assemblage. Since it occurred in a very short period of time, it is more likely to be due to a change in behavior rather than the recruitment of new individuals, as the pattern is consistent for both biomass and density. Recent studies have found how fish are able to discern between scuba divers and spearfishing divers, and behaviourally respond to increased spearfishing pressure by being more shy and elusive (Sbragaglia *et al.* 2018). Also, it has been documented that increasing depth acts as fishing refuge as most fishing techniques focus on shallow waters (Tyler *et al.* 2009, Goetze *et al.* 2011). In this sense, it is possible that during the period in which poaching was high and surveillance was cut off, fish behaviour changed and individuals moved to deeper rocky reefs, recovering their natural depth ranges once surveillance had returned to their previous levels, and thus being detected again by the routine monitoring UVCs of the marine reserve.

Regional comparison of fish biomass

If we compare the values of biomass carrying capacity estimated in this MPA for the whole study period with the range of values available in the literature, we find that the recorded biomasses in Cabo de Palos-Islas Hormigas are disproportionately high. For instance, Sala *et al.* (2012) found that the maximum fish total biomass recorded in their dataset, issued from 13 MPAs and 17 unprotected areas across the Mediterranean (data that were reused by Guidetti *et al.* 2014), was 118.3 g m^{-2} in Tavolara, while in our study the carrying capacity reached remarkable 757.6 g m^{-2} (Table 3); regarding the biomass of apex predators, Sala *et al.* (2012) found 236.1 g m^{-2}, while here we estimated that carrying capacity of piscivourous species reached 651.2 g

m^{-2}. For their part, Coll *et al.* (2013) found a maximum biomass of fish in the MPAs of Es Freus, Palma bay and Northern Menorca MPAs of 23.24 g m^{-2}. Also, García-Rubies *et al.* (2013) in Medes Islands found a maximum fish biomass of 72.87 g m^{-2} for the total fish species vulnerable to fishing (including the species *E. marginatus*, *D. cervinus*, *D. labrax*, *D. dentex*, *S. aurata*, *S. umbra*) (values obtained from the published figures through the GetData Graph Digitizer software, available at http://getdata-graph-digitizer.com). This difference could be even greater if we consider that the predatory fish populations probably did not reach their carrying capacity in the area due to poaching, as explained above.

The disproportionate difference in abundance and biomass of reef fish (mainly high-level predators) with other areas (either protected or not) in the region could be explained in part, in addition to a particularly intense reserve effect, by different non-exclusive hypotheses, namely: primary-productivity effect, depth effect, habitat effect, 'supply-side' effect, and/or energetic-subsidies effect, as briefly developed below.

Primary-productivity hypothesis

Local primary productivity could affect the dynamics of fish populations in the Mediterranean Sea by bottom-up processes (Piroddi *et al.* 2017). A gradient of primary production has been hypothesized to occur from south to north in the Southwestern Mediterranean basin, based on oceanographic literature, being maximum in the Alboran Sea and minimum the Balearic islands (García-Charton *et al.* 2004, Rojo *et al.* in prep.), which could be reflected in the fish biomass that each location is able to support. Large-scale studies by García-Charton *et al.* (2004) and Rojo *et al.* (in prep.) corroborate in part this hypothesis, but give the Cabo de Palos-Islas Hormigas marine reserve high biomass values that do not correspond to its position in the aforementioned gradient. Therefore, other factors are likely to concurrently act to explain the observed differences.

Sampling-depth hypothesis

It has been found that there is a tendency of large-sized individuals to live at deeper areas as a consequence of ontogenetic movements aimed at benefit from decreasing

metabolic rates at lower temperatures (Macpherson and Duarte 1991), and as a way to differentiate their habitat niche as they grow (Hackradt 2012). Our study was performed at depths between 16 and 20 m, while Sala *et al.* (2012) sampled rocky habitats at 8-12 m; for their part, Coll *et al.* (2013) performed UVCs at 3-15 m depth, and García-Rubies *et al.* (2013) spanned their sampling units between 10 and 20 m depth; therefore, this methodological difference could partly contribute to explain the differences found.

Habitat-structure hypothesis

The singular arrangement of rocky reefs in this MPA, formed by steep and pointed rocky shoals and islets, could determine exceptionally large values of density and biomass of predatory species, as far as structural habitat is an important determinant of fish assemblage structure (species composition and relative abundances) (García-Charton *et al.* 2000). In a multi-scale spatial study, García-Charton *et al.* (2004) found that part of the observed variability in fish assemblage structure in seven locations (encompassing a geographic range of about 400 km of latitude by about 500 km of longitude) can be explained in part by fine-to-medium scale differences in habitat structure. Rocky, complex habitats favor the development of diverse and abundant reef fish fauna, because at fine scale they provide a multitude of gaps, cracks and fissures where demersal fish can find resources (namely refuge and food) and at medium-scale they determine steep profiles and a rugged topography.

In the case of pelagic fish species, they could be attracted by the vertical and steep rocky masses: big schools of large-sized greater amberjacks (*Seriola dumerili*) and common dentex (*D. dentex*) are observed around the rocky shoals for a good part of the year, as a likely realization of the "spatial reference hypothesis" (Fréon and Dagorn 2000) to explain the concentration of schooling pelagic fish around seamounts, islands or banks. The fact that the 'reserve effect' on biomass is detectable for both the total and total reduced descriptors corroborate that pelagic species are an intrinsic part of the fish assemblage in the area, regardless of the protection measures.

'Supply-side' hypothesis

Fluctuations in spatial and temporal patterns of reef fish larval dispersal (Leis 2007, Llopiz *et al.* 2014) determine population connectivity (Calò *et al.* 2013, Martí-Puig *et al.* 2013, Bryan-Brown *et al.* 2017) and subsequent changes throughout the different early-life history stages of fishes, such as settlement and recruitment (Félix-Hackrad *et al.* 2013). These processes can have profound influence on the size of adult populations (Roughgarden *et al.* 1988), both inside and outside MPAs (Balbar and Metaxas 2019). Studies carried out in our study area (Félix-Hackradt *et al.* 2013a, 2013b, 2014) found a significant spatial variability of both post-larval supply and density and structure of fish settlers and recruits, likely to be due to spatial distribution of habitat types and variability in habitat structure. Thus, singular habitat distribution and variations in structure within the marine reserve could determine differential fish assemblages compared to neighbouring unprotected locations. In addition, the few connectivity studies made in the area using different methodologies (genetics, otolith microchemistry, larval dispersal models) point to different situations depending on the species, so that for *Oblada melanura* the studies depict a relatively open state, although with some dependence on neighboring sites (Calò *et al.* 2016a, 2016b, 2018). However, for *E. marginatus* the local situation appears to be one of self-replenishment, together with functioning as a source of propagules to other locations in the region (Orenes *et al.* in prep.), which may explain the patterns found.

Energetic-subsidies hypothesis

The huge observed difference in fish biomass between Cabo de Palos-Islas Hormigas and other Mediterranean locations could be also explained by the contribution of energetic subsidies to the local food web as determinants of the trophic structure (Trebilco *et al.* 2013, Barneche *et al.* 2014).

On the one hand, huge schools of forage species such as *Boops boops* and *Engraulis encrasicolus* are typical in the area, where they can stay for weeks and even months during late summer and autumn (Rojo & García-Charton, *personal observation*); such concentrations could be caused by the strong water currents and swirls determined by the steep topography of rocky shoals and islands and tough

oceanographic processes occurring in the area, which in turn could cause locally increased primary productivity and associated increment in zooplankton biomass. Also, very high abundances of the damselfish *Chromis chromis* are observed in the area. Different demersal predatory species such as groupers (*Epinephelus* spp., *Mycteroperca rubra*) and the sparid common dentex, as well as mesopredators such as combers (*Serranus* sp.), among other species, are recurrently observed preying on the abundant food resource determined by the abovementioned myriad of small-bodied pelagic fishes living in the area (I. Rojo & J.A. García-Charton, *personal observation*), thus supporting their role as food suppliers to reef fish communities (Beaudreau & Essington 2011, Trebilco *et al.* 2016). Moreover, the damselfish *Chromis chromis* is a key species in local Mediterranean food webs as resource cycler from the water column to the benthos, and also as prey resource for piscivorous predators (Pinnegar 2018), which could also support this pelagic-fish subsidy hypothesis. In fact, we have repeatedly observed damselfish individuals being regurgitated by adult dusky groupers (*E. marginatus*) when being handled in telemetry studies (C. W. Hackradt, *personal observation*), thus corroborating the importance of this species as prey in the local food web.

On the other hand, another possible source of energetic subsidies to the protected rocky reefs is the movement pattern of highly mobile piscivorous fishes to forage outside the MPA (Williams *et al.* 2018). In our case, large amounts of greater amberjacks and common dentex are frequently caught by small-scale fishing gears outside the MPA (Esparza 2010), thus demonstrating that these movements from the marine reserve to neighbouring unprotected sites effectively occur.

The Cabo de Palos - Islas Hormigas marine reserve as a pristine ecosystem

Traditionally, MPAs have been proposed as proxies for pristine ecosystems, provided that they are well managed. In the absence of anthropogenic disturbance, MPAs are expected to resemble what natural conditions would look like decades ago (McClanahan *et al.* 2007). Recently, though, some studies have highlighted that it may be not that true. For example, it was found that wilderness areas far from human influence harbored 3.5 times more biomass of top predators than the largest (17 500

ha), oldest (38 years of protection) and well enforced MPA in New Caledonia (D'agata *et al.* 2016). For their part, McClanahan *et al.* (2019) found that remote tropical reefs (> 9 hours travel from fishing markets) from the Indian and Pacific Ocean had substantially greater biomass than old (> 15 years) and highly-compliant fisheries closures. Although the Cabo de Palos-Islas Hormigas marine reserve probably did not reach its carrying capacity due to pressure from poaching, it houses the highest values of fish biomass by far in the entire region, indicating the high effectiveness of this marine reserve in terms of population recovery. It is unlikely, however, that it can resemble a pristine ecosystem, as some predatory species such as monk seals and sharks are absent in the area (Sala 2004, Maynou *et al.* 2011, Sala *et al.* 2012).

In conclusion, our study, although focusing in one single Mediterranean MPA, give important insights to the long-term effects of protection on reef fish assemblages. After 23 years of protection this MPA has exerted a strong positive influence on the biomass of the whole reef fish assemblage, as well as the density and biomass of predatory and medium-IF species. This effect has taken 10 to 15 years to reach a magnitude close to the maximum observed to date. On the other hand, a likely occurrence of top-down process may have reduced the abundance and biomass of lower trophic groups. Moreover, commercial value solely is not a good indicator for the recovery of the species, and other biological and ecological features must be taken into account. High enforcement is essential to achieve the recovery of the populations and modifying enforcement levels can vary the recovery trajectories; the occurrence of continuous episodes of poaching for several years has likely prevented the protected area from reaching its carrying capacity, so it is not yet known how long the abundances and biomass of the populations most benefited by the protection measures could continue to grow. Even so, the biomass of fish reached are much higher than those situated at the upper end of the range of variation of the values recorded so far in the Mediterranean, so that several non-exclusive hypotheses (primary productivity, sampling depth, habitat structure, 'supply-side' effects, energetic subsidies) could account for the observed patterns. The continued monitoring of this marine reserve in the coming years is more necessary than ever, in order to better understand the mecanisms underlying the exceptional response of the

reef fish assemblage to protection measures. In addition, complementary studies such as functional (Villéger *et al*. 2017, Rincón-Díaz *et al*. 2018) and tropho-dynamic (Prato *et al*. 2014) modelling of the reserve effect, as well as diet studies through stable isotopes (Funes *et al*. 2018), would help to fully understand the changes that have occurred among the trophic groups as a result of protection, and to explain the exceptionally high biomass values observed througout time.

5. Appendices

Appendix A. Number of sites and replicates per site performed in the Cabo de Palos-Islas Hormigas MPA along the period of study.

Year	N sites	N replicates per site	Total replicates
1996	5	3	15
1997	5	2	10
1998	5	3	15
1999	-	-	-
2000	1	3	3
2001	-	-	-
2002	5	3	15
2003	6	1-3	14
2004	5	3	15
2005	6	3	18
2006	5	3	15
2007	6	3	18
2008	6	3	18
2009	6	3	18
2010	4	3	12
2011	-	-	-
2012	-	-	-
2013	6	3	18
2014	5	3	15
2015	6	2-3	17
2016	7	3	21
2017	7	3	21
2018	7	3	21

CHAPTER 3

Effects of the sampling methodology on the detection of protection benefits on predatory fish

Effects of the sampling methodology on the detection of protection benefits on predatory fish

1. Introduction

High-trophic level predatory fishes (i.e. groupers, snappers, jacks, etc.) play a key role in marine ecosystems (Baum & Worm 2009). These species have been historically targeted by fisheries and are currently depleted or even completely absent in coastal ecosystems (Jackson 2008, Piroddi *et al.* 2017). In fact, in the absence of fishing pressure, predators show stronger benefits to protection when compared to other trophic level species (Micheli *et al.* 2004, Guidetti *et al.* 2014, Edgar *et al.* 2014).

Marine Protected Areas (MPAs) have been proposed worldwide as an effective tool for the conservation of the biodiversity and fisheries management (Pérez-Ruzafa *et al.* 2017). In general, MPAs show positive effects on the recovery of density and biomass of exploited fishes, especially those with large sizes, located at higher trophic positions, and having commercial importance (Mosquera *et al.* 2000, Côté *et al.* 2001, Micheli *et al.* 2004, Guidetti & Sala 2007, Claudet *et al.* 2008, Guidetti *et al.* 2008, Sciberras *et al.* 2013, Hackradt *et al.* 2014, Rojo *et al.* 2019).

Ecological monitoring is essential to understand the functioning of MPAs (Roberts *et al.* 2018). Worldwide, underwater visual censuses (hereafter UVC) have been adopted as routine monitoring tools to assess fish assemblages in MPA evaluations since they are non-destructive, cost-efficient and allow the detection of a high number of species (García-Charton *et al.* 2000, Edgar *et al.* 2004, Prato *et al.* 2017). Traditionally, UVCs have been mostly performed by using conventional strip (belt) transects (hereafter, CST; e.g. Harmelin 1987, García-Rubies & Zabala 1990, García-Charton *et al.* 2004, Hackradt *et al.* 2014), in which sampling area is delimited both in length (typically between 25 and 50 m) and width (usually between 2 and 5 m), and every individual encountered is recorded. Other sampling techniques commonly used include stationary point counts and roaming censuses, among others (García-Charton *et al.* 2000, Irigoyen *et al.* 2018).

Several adaptations of UVC methods have been proposed to focus on particular groups of fishes, such as the case of charismatic, ecologically and commercially important species of medium and large size. Such improvements seek, on the one hand, to achieve a better detection of spatial and temporal changes (Kulbicki & Sarramégna 1991, Lynch *et al.* 2015), and secondly, to provide more accurate and realistic estimates of biomass, diversity, species richness and population size at a given location (Ward-Paige *et al.* 2010, Thanapoulou *et al.* 2012, Loiseau *et al.* 2016, Prato *et al.* 2017, Irigoyen *et al.* 2018). As a result of these efforts, some important ecological findings have been recently revised. For instance, Bradley *et al.* (2017) found a likely 56% overestimation of shark biomass in the remote Palmyra atoll compared to previous studies due to the bias associated with the UVC techniques used so far. Consequently, they came to the conclusion that the previous concept of an inverted biomass pyramid of top predators in pristine marine ecosystems might not be as correct. Therefore, it is essential to understand the biases associated with the different methodologies to census predatory fishes and how they may alter the results and the estimates of population demographic parameters.

Regardless of the shape, size and other characteristics of the sampling units, UVC techniques are generally applied assuming that all fishes present within the surveyed surface will be detected by the observer (probability of detection = 1; Bukland *et al.* 2001). However, the probability of detection may be lower than previously thought, as pointed out by MacNeil *et al.* (2008), who found that the visual detectability of almost 50 fish families in Tanzanian waters varied between 0.05 and 0.54. Moreover, the ecology and behaviour of the species may contribute to increase the bias of the estimates: rare or shy species, and/or those patchily distributed, as is the case of many high level predators, are more likely to remain undetected (Kulbicki 1998, Bozec *et al.* 2011, Goetze *et al.* 2017), increasing the probability of having false absences. Thus, if the methodology applied leads to the collection of biased estimates, assessments of the biodiversity, the structure of the communities and the population size may be inadequate.

Many attempts have been made to adapt the existing methodologies to maximize species detectability, such as increasing the number of observers (Bernard *et al.* 2013, Issaris *et al.* 2012) or sampling replicates (MacNeil *et al.* 2008). Other authors proposed to increase the size of the transects: for example, Harmelin-Vivien *et al.* (2015) performed 50×15-m^2 transects to study the abundance of the brown meagre (*Sciaena umbra*) in the Nature Reserve of Scandola (Corsica, Western Mediterranean). For their part, Prato *et al.* (2017) proposed transects of different widths according to the target group, and found that 20-m wide transects gave more precise estimates than those of 5 m for density and biomass of Mediterranean predatory fish species. Also, sampling techniques have been further developed in order to increase the accuracy of data (Katsanevakis *et al.* 2012), such as the combination of UVC with mark and recapture methods (Hackradt 2012), repeated presence-absence surveys for occupancy models (Issaris *et al.* 2012), removal methods (Söffker *et al.* 2015), distance sampling (Kulbicki & Sarramégna 1991, Irigoyen *et al.* 2018) and GPS-tracked roaming transects (Beck *et al.* 2014, Lynch *et al.* 2015, Irigoyen *et al.* 2018, Wong *et al.* 2018).

Particularly, it has been shown that GPS-tracked roaming transects increase the efficiency of UVC by covering 33–75% more area than CST for a comparable diving time (Beck *et al.* 2014, Lynch *et al.* 2015, Irigoyen *et al.* 2018), because there is no diving time investment on rolling the census tape and there is not transect length limitation, since the transect path is automatically recorded by a GPS above the diver. This method is especially useful as it allows sampling very sparse populations that might otherwise require much more effort to get a record and even still remain undetected. Additionally, using wider transects, and especially distance sampling methods, in which perpendicular distance from the transect line is estimated on large census area widths (Kulbiki & Sarramégna 1991, Buckland *et al.* 2001; see details below), would lead to more accurate and precise estimates when compared to CST. This is critical when sampling species that may react to the presence of divers (either attractive or elusive behaviour), and hence when comparing among sites with different levels of human disturbance.

On the other hand, it is essential to assess which MPA features favour the recovery of this group of fish species (Rojo *et al.* 2019). One of the most debated

attributes of MPAs is the adequacy or not to implement partially protected areas - or buffer zones, allowing extractive activities to different degrees (Sala & Giakoumi 2017). While the efficacy of fully protected areas - or no-take zones as conservation measures has been widely accepted (Claudet *et al.* 2008, Edgar *et al.* 2014, Friedlander *et al.* 2017), there is still controversy on the role of buffer zones, which are expected to be less effective than fully protected areas (Lester & Halpern 2008, Lester *et al.* 2009, Sciberras *et al.* 2013, Giakoumi *et al.* 2017, Sala & Giakoumi 2017). Indeed, according to some authors, buffer zones might even exert a negative effect on conservation purposes because some kinds of fisheries are allowed inside them, which may diminish the global conservation effects (Claudet *et al.* 2008, Sciberras *et al.* 2013). However, it has been recently found that buffer zones may produce considerable ecological benefits provided that they are well regulated and located adjacent to a no-take zone (Hackradt *et al.* 2014, Abecasis *et al.* 2015, Zupan *et al.* 2018). In the Mediterranean Sea, around 92% of the MPAs consist of multiple protection areas, with either one or several of both no-take and buffer zones (Gabrié *et al.* 2012), thus understanding the ecological effects of both protection levels is crucial for management purposes.

The aim of the present study was to compare the performance of different sampling methodologies, namely CST and GPS-tracked roaming transects combined with distance sampling (hereafter TRT+DS; Irigoyen *et al.* 2018), and fixed-width derived transects, to measure the effects of protection, including no-take and buffer zones, in terms of richness, density and biomass of high level predatory fish in 5 Mediterranean MPAs. On the basis of the previous literature, we hypothesise that longer and wider transects will result in more accurate and realistic estimates. Moreover, we expect no-take zones to exert a stronger protection effect than buffer zones. Our results will help to identify the most accurate and realistic method for the study of predatory fishes and consequently to provide better assessments of MPA effects on this trophic group.

2. Material and methods

2.1. Study areas and sampling design

The study was carried out in the summers of 2016 and 2017 in five MPAs located in the Western Mediterranean Sea, from south to north: Cabo de Gata-Níjar marine reserve (hereafter Cabo de Gata), Cabo de Palos-Islas Hormigas marine reserve (Cabo de Palos), Isla de Tabarca marine reserve (Tabarca), Es Freus d'Eivissa i Formentera marine reserve (Es Freus), and North of Menorca marine reserve (Menorca) (Fig. 1, Appendix A). Each MPA consists of one or several no-take zones, where all activities are banned except scientific research (subject to administrative authorization), and a buffer zone, where certain human activities, such as small-scale fishing and recreational diving, are allowed but strongly regulated. In addition, we included in the study adjacent unprotected areas with habitat characteristics comparable to their corresponding MPA.

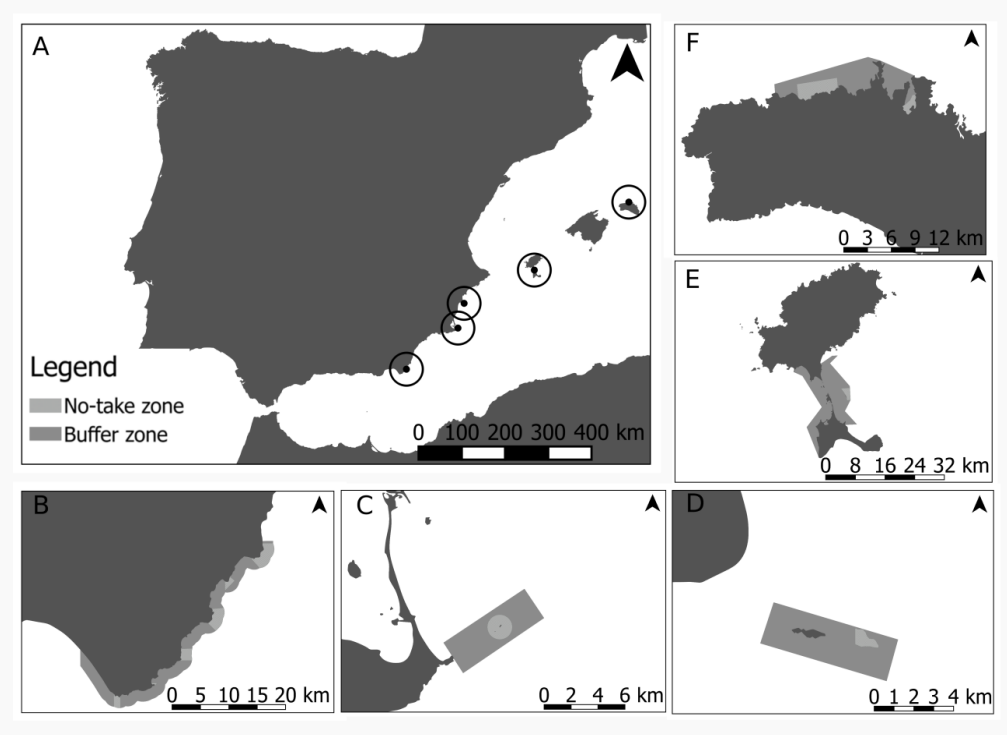


Figure 1. Location of the MPAs sampled in the coast of Spain (A): Cabo de Gata MPA (B), Cabo de Palos-Islas Hormigas MPA (C), Tabarca MPA (D), Es Freus MPA (E) and Norte de Menorca MPA (F). No-take zones (light gray) and buffer zones (dark gray) are highlighted in the maps.

Within each protection level (no-take zone, buffer zone, unprotected areas) of each location we randomly selected several sites separated by hundreds to thousands of meters, in order to control the spatial variability at medium scale of the measured parameters. Sites were characterised by being rocky reefs located both in coastal cliff areas and on islands or rocky outcrops that do not reach the surface. The number of sites selected in each protection level was proportional to the available habitat, so that, in general, the sampling design consisted of three sites within each no-take zone, six inside each buffer zone and nine in the unprotected areas, as in all cases no-take zones are smaller than the other zones. As exceptions, only six unprotected sites were sampled in Tabarca and Es Freus due to the lack of suitable habitats outside these MPAs. In each site, three haphazardly distributed replicates by each sampling technique, separated at least 20 m in order to avoid spatial dependence, were performed. Replicates consisted on fish UVCs using two different methodologies: CST and TRT+DS, for which we considered only predatory large-sized economically important fish species occupying high trophic levels in Mediterranean coastal ecosystems (see below). The procedure to randomly place sampling replicates was constrained to include comparable habitats, consisting as much as possible of steep rocky bottoms with small and medium sized boulders interspersed in some sites by patches of *Posidonia oceanica*, surrounded by soft bottoms and seagrass meadows at 25-35 m depth. In general the replicates were conducted at depths between 13 and 18 m, with the exception of some sites in Tabarca and Cabo de Gata MPAs and their respective unprotected areas, in which rocky reefs deeper than 6-10 m depth are very scarce. Visual censuses were carried out by experienced divers at daytime between 10.00 am and 3.00 pm, when light and water conditions were optimal.

2.2. Sampling methods

In the case of CST, transects of 50 m length (measured by a tape) and 5 m width (2.5 m at each side of the diver, estimated visually) (i.e. covering a surface of 250 m^2) were performed. All fish observed in the sampled area were recorded, annotating the name of the species, and the number and size of the individuals observed. Abundance was assigned to one of nine predetermined abundance classes for which the limits coincide with the terms of a base ~ 2 geometric series (1, 2–5, 6–10, 11–30, 31–50, 51–100,

101–200, 201–500, > 500; Harmelin 1987) (see García-Charton *et al.* 2004, for further details of the sampling protocol used). From these data, only the abundance of large predatory species was retained for subsequent analysis.

For the TRT+DS method, two divers performed transects of variable lengths following an imaginary line at a constant depth contour while pulling a GPS located on a body-board on the surface. The tracks were recorded by the GPS, and the distance covered along each transect was extracted by geo-referencing start/end census points with a synchronized clock. Transects lasted about 8 minutes on average, which gave a mean transect length of 110 m (± 2 m SE) in an equivalent diving time to CST. Each diver surveyed a 20-m band on their respective side from the imaginary line; thus, for a total of 40-m width, transects covered an average surface of 4400 m^2. Only predatory species (Appendix B) were included in the visual censuses. Similarly to the case of CST, for each observation the name of the species was noted, the number of individuals was counted and first-sight perpendicular distance in 1-m intervals between every fish observed and the imaginary line was estimated, either for single individuals or groups. Fish moving from one side to the other were noted and cross-checked between the two divers after the sampling in order to avoid double counts of individuals (see Irigoyen *et al.* 2018, for further details of the sampling protocol used).

Both in CST and TRT+DS fish lengths were estimated in 5-cm size classes (Harmelin-Vivien *et al.* 1985).

2.3. Response variables and estimators

From both CST and TRT+DS methods, the predatory fish assemblage was specified by its species richness (number of species), density (number of individuals 100 m^{-2}) and biomass (in g 100 m^{-2}) using different methodologies (see below). The latter was calculated through adequate length-weight relationships from local studies when available (Morey *et al.*, 2003), otherwise data obtained from FishBase (Froese & Pauly 2017) were used.

2.3.1. Conventional Strip transects (CST)

To calculate density in each CST, geometric means of fish abundance classes were used as class marks (García-Charton *et al.* 2000, 2004). Thus, for each species in each transect, the resulting abundance is the sum of the geometric means of the abundance class of each observation (individual or group); as originally observations are made in a transect of 50×5 (=250) m^2, to allow comparisons with other sampling techniques density was re-calculated by transforming the obtained value to be referred to a surface of 100 m^2.

2.3.2. Tracked Roaming Transects with Distance Sampling (TRT+DS)

Distance sampling theory (DS) allows the estimation of density (i.e. number of individuals per unit of area) of biological populations based on the recorded distances from each individual to a randomly placed line. The detection function g(*y*) is the probability of detecting an object, given that it is at a perpendicular distance (*y)* from the line (Buckland *et al.* 2001). The g(*y*) decreases as *y* increases, always being $0 \leq g(y) \leq 1$, and assuming that g(0) = 1 (i.e. the probability of detecting and object right on the line is 1). Thus, although a large proportion of objects may be undetected, by adjusting the sightings to the g(*y*) detection function it is possible to calculate reliable estimates of the true density (Burnham *et al.* 1980, Buckland *et al.* 2001). DS theory requires at least 30 records to calculate trustworthy densities (Buckland *et al.* 2001, 2004). Most transects, however, had less than 30 records for each species (especially in unprotected areas). As a consequence, in order to graphically represent the densities taking into account the detection probability function, the calculations were made considering the most abundant species pooled (see below), so that only one density value has been provided for each MPA and protection level. Calculations were made through the free software DISTANCE 6.2 (Thomas *et al.* 2010).

For statistical modelling purposes, the densities were calculated using a series of estimators derived from the data taken with the TRT+DS method, but without taking into account the detection function g(*y*), as detailed below.

Firstly, an encounter rate (*ER*) was calculated in each transect *i* as the number of individuals of all preselected species recorded (n_i) per meter of transect length (L_i) as measured with the GPS track (i.e. $ER_i = n_i/L_i$). This estimator has been widely used as an appraisal of distance-calculated densities in terrestrial ecology when DS theory do not allow to make calculations at the transect level due to a too low abundance of the recorded species (Burgi *et al.* 2011, Nabte *et al.* 2013).

Secondly, a value of density was calculated through the average distance method (*AD*). This estimator considers the distance at which individuals were recorded but, contrary to the DS theory, no function is applied to the histograms of sighting distances. Instead, it calculates mean distances and refers the abundance to the area of average distance as follows: $AD_i = [n_i/(2Ld_i)]$, with $d_i = \left({}^{1}/_{n_i}\right) \sum_{j=1}^{n_i} d_{ij}$ (Kulbicki & Sarramégna 1999). In order to be able to compute the formulae, the minimum width ($2d_i$) at which each observation has been recorded is 1 m, even in the cases of those fishes that were seen directly on the imaginary line (i.e. at distance 0); in that cases, the resulting density value (standardized to number of individuals per 100 m^2) was kept as the one representing the whole transect (even when $2Ld_i < 100$ m^2, because $L <$ 100 m), since additional records were certainly not made at distances greater than 0.5 m from the census imaginary line.

Finally, Tracked Roaming Transects of fixed widths were considered by including the fishes seen within distances ≤ 3, 5, and 10 on each side of the imaginary line over which the visual census was made. Fixed width transects larger than 20 m (10 m from each side of the line) were not included because the probability of detection dropped sharply after that distance. A similar decline in the probability of detection has been previously found (Bozec *et al.* 2012) and is the maximum width adopted in similar studies (Prato *et al.* 2017). Densities D_i were calculated as $D_i = n_i / (L_i \times W)$, with L_i being the transect length (i.e. the GPS track), *W* the widths of 6, 10 and 20 (called TRT6, TRT10 and TRT20, respectively), and n_i the number of individuals of the species sighted in each case.

For each response variable different estimators were taken into account. Richness and biomass data were analysed through TRT20, TRT10, TRT6 and CST. For

density data, though, formal analyses were done through the estimators *ER*, *AD*, TRT20, TRT10, TRT6 and CST.

2.4. Data analysis

We applied generalized linear mixed models (GLMMs; Zuur *et al.* 2009) to explore the factors affecting the richness, density and biomass of predatory fish in Mediterranean MPAs. We performed different analyses for each of the methodology or estimators and response variables, as estimators within a response variable were not independent among them. For the density and biomass analyses we retained the species that appeared in at least 10% of the total transects performed including the two methodologies (Appendix A) and evaluated them pooled together. This allowed us to assess differences among MPAs and protection levels without having the effect of rare species. The species included were *Epinephelus marginatus*, *Epinephelus costae*, *Mycteroperca rubra*, *Dentex dentex*, *Sphyraena viridensis*, *Sciaena umbra* and *Muraena helena* (Appendix A); the latter was excluded for the biomass analyses because they appeared mostly in cracks in the rocks, so it was not possible to estimate their lengths.

Models included the factors Location [fixed, with five levels (the different MPAs and their unprotected counterparts); Protection level [fixed, with three levels (no-take, buffer and unprotected)]; the interaction among Zone and Protection Level; and Site, (random, with a variable number of levels depending on the location, see above). Location was considered to be a fixed factor because we hypothesize that there is a gradient of primary production, reaching maximum values in the Alboran Sea and decreasing northwards and offshore from the mainland to the Balearic Islands (García-Charton *et al.* 2004). Indeed, the Alboran Sea has the greatest levels of primary productivity due to phytoplankton uptake of nutrients upwelled at Gibraltar and the cyclonic circulation cells (Lazzari *et al.* 2012; García-Martínez *et al.* 2019). Moreover, there is a coastal-island gradient due to permanent frontal structures combined with river runoff and upwellings created by submarine canyons (Estrada *et al.* 1996). In fact, Menorca island has been found to be one of the most oligotrophic areas in the western Mediterranean Sea (Cardona *et al.* 2007) due to phosphorus limitations because of the occurrence of oceanographic gyres (García-Martínez *et al.* 2019).

Arguably, primary production is the most important environmental factor determining the production of marine fishes (Pauly & Christensen 1995, Watson *et al.* 2013, Piroddi *et al.* 2017). Thus, accounting for this hypothesis, the factor Location would represent discrete steps along a gradient of primary production determining fish density and/or biomass, as far as this environmental variable would follow the pattern Cabo de Gata > Cabo de Palos > Tabarca > Es Freus > Menorca. Consequently, and because all factors are categorical, we set the reference values for the Cabo de Gata MPA (i.e. the location with the higher primary productivity) and the unprotected protection level (in theory, the level harbouring the lower values of density and biomass), thus analyses are made according to them.

For the richness response variable we used Poisson error distributions and log-link functions. We applied the glm() and glmer() functions of the packages stats (R Core Team 2015) and lme4 (Bates *et al.*, 2015), respectively. For the density and biomass response variables we applied the glmmTMB() function from the glmmTMB package (Brooks *et al.* 2017) in which models are fitted using maximum likelihood estimation and random effects are integrated using the Laplace approximation. This package has been recently developed and is more flexible than other packages to deal with zero-inflation and overdispersion on the non-zero data (Brooks *et al.* 2017). We modelled raw abundance and biomass per transect using negative binomial distributions and log-link functions, and included the area covered by each transect as an offset parameter. In all cases, we constructed all model combinations, including the "null model" without the random factor. Model selection was based on Akaike's information criteria (AIC). We selected the model with the lowest AIC, and when Δ AIC was ≤ 2 we selected the simplest model (Burnham & Anderson 2002). Significant terms were considered when $P \leq 0.05$. Model validation was done through visual inspection of residual plots and Shapiro tests for deviations from homoscedasticity and normality, respectively. When outliers were present we analysed them and when convenient they were excluded and the models were redone. We evaluated the performance of the final models by means of the marginal R^2, which measures the variability accounted by the fixed terms of the model (Nakagawa & Schielzeth 2013). We used the function r2()

from the sjstats package (Lüdecke 2018). All analyses were performed in R (R Core Team 2015).

Additionally, in order to understand how the limitation in transect widths may affect the detection by each of the estimators we calculated mean detection distances for each of the species in the study in the different protection levels for all MPAs pooled.

3. Results

3.1. Predatory fish assemblage

A total of 252 transects with each methodology were carried out along the five MPAs. The complete set of predatory species recorded in the whole study includes *Caranx crysos*, *Dentex dentex*, *Dicentrachus labrax*, *Epinephelus marginatus*, *Epinephelus caninus*, *Epinephelus costae*, *Euthynnus alletteratus*, *Muraena helena*, *Mycteroperca rubra*, *Pagrus pagrus*, *Sarda sarda*, *Sciaena umbra*, *Scorpaena scrofa*, *Seriola dumerili*, *Sparus aurata*, *Sphyraena* spp., *Myliobatis aquila* and *Torpedo marmorata* (Appendix B). The number of species recorded by the CST, the TRT+DS and their derived estimators differed according to the MPA and the protection level considered, as did the values obtained for the density and biomass (Fig. 2), as developed below.

3.2. Effect of protection on the species richness of predatory fish

For any location and protection level considered, the estimators covering greater areas per transect tended to yield higher values of richness (i.e. more species detected with the estimator; TRT20 > TRT10 > TRT6 > CST; Fig. 2a). AIC did not differ among the GLM and GLMM models for richness, indicating the absence of effect of the factor Site. The results of GLM applied to the number of predatory fish species measured by the CST method showed that the response of this assemblage to protection level varied depending on the location considered (as shown by the significant interaction between particular Locations and Protection levels, while it was non-significant when measured through the TRT6 method). The TRT20 and TRT10 models included the interaction but

none of the specific terms were statistically significant (Table 1). Regarding the interaction, CST showed that richness was higher in the buffer and no-take zone of Cabo de Palos, as well as in the buffer zone of Menorca and Tabarca (Table 1). Moreover, regarding the main effects, data obtained with methods TRT20 and TRT10 showed that species richness was significantly greater in no-take zones, while the data obtained with TRT6 detected significantly higher values of species richness in both no-take and buffer zones. Additionally, Cabo de Palos and Es Freus harboured higher species richness than the other locations (positive and statistically significant results, all protection levels considered together, Table 1) with all census methods, apart from the case of the data obtained with CST. The R^2 of the final models were around 50% for all the estimators considered (Table 1).

Table 1. Results of the GLMs for the estimators applied (TRT20, TRT10, TRT6 and CST) showing the variables explaining fish species richness, based on model selection. Models excluded by AIC are not shown in the table.

	TRT20			TRT10			TRT6			CST		
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-0.08	0.20	0.70	-0.25	0.22	0.25	-0.61	0.17	**<0.001**	-0.25	0.22	0.25
LOC CP	1.07	0.23	**<0.001**	1.11	0.25	**<0.001**	1.31	0.17	**<0.001**	-0.97	0.42	**0.02**
LOC EF	0.95	0.25	**<0.001**	1.00	0.27	**<0.001**	1.14	0.18	**<0.001**	0.25	0.32	0.43
LOC MN	-0.17	0.30	0.56	-0.10	0.32	0.75	0.09	0.21	0.68	-0.85	0.40	**0.03**
LOC TA	-0.17	0.33	0.60	-0.34	0.38	0.38	0.25	0.21	0.24	-0.56	0.42	0.18
PL BZ	0.28	0.29	0.34	0.14	0.33	0.69	0.62	0.12	**<0.001**	0.19	0.33	0.55
PL NT	0.82	0.30	**0.01**	0.89	0.33	**0.01**	0.84	0.13	**<0.001**	0.76	0.39	**0.02**
LOCCP: PLBZ	0.10	0.34	0.77	0.32	0.38	0.40				2.29	0.50	**<0.001**
LOCEF: PLBZ	0.17	0.35	0.64	0.42	0.39	0.28				0.13	0.45	0.77
LOCMN: PLBZ	0.69	0.40	0.08	0.66	0.45	0.14				1.19	0.51	**0.02**
LOCTA: PLBZ	0.42	0.44	0.34	0.86	0.50	0.08				1.42	0.51	**0.01**
LOCCP: PLNT	-0.05	0.35	0.90	-0.02	0.38	0.97				1.81	0.52	**<0.001**
LOCEF: PLNT	-0.53	0.39	0.18	-0.46	0.41	0.26				0.09	0.47	0.86
LOCMN: PLNT	-0.13	0.46	0.78	-0.17	0.49	0.73				-0.25	0.65	0.70
LOCTA: PLNT	0.63	0.44	0.16	-0.64	0.50	0.20				0.69	0.55	0.21
AIC	821.34			776.92			729.11			663.70		
Marginal R^2	0.52			0.55			0.54			0.54		

LOC: location. CP: Cabo de Palos. EF: Es Freus. MN: Menorca. TA: Tabarca. PL: protection level. BZ: buffer zone. NT: no-take zone. The final models were: Estimator ~ ZN * PL + ZN + PL. The estimate (including the sign), standard error and p-value of the parameters are shown.

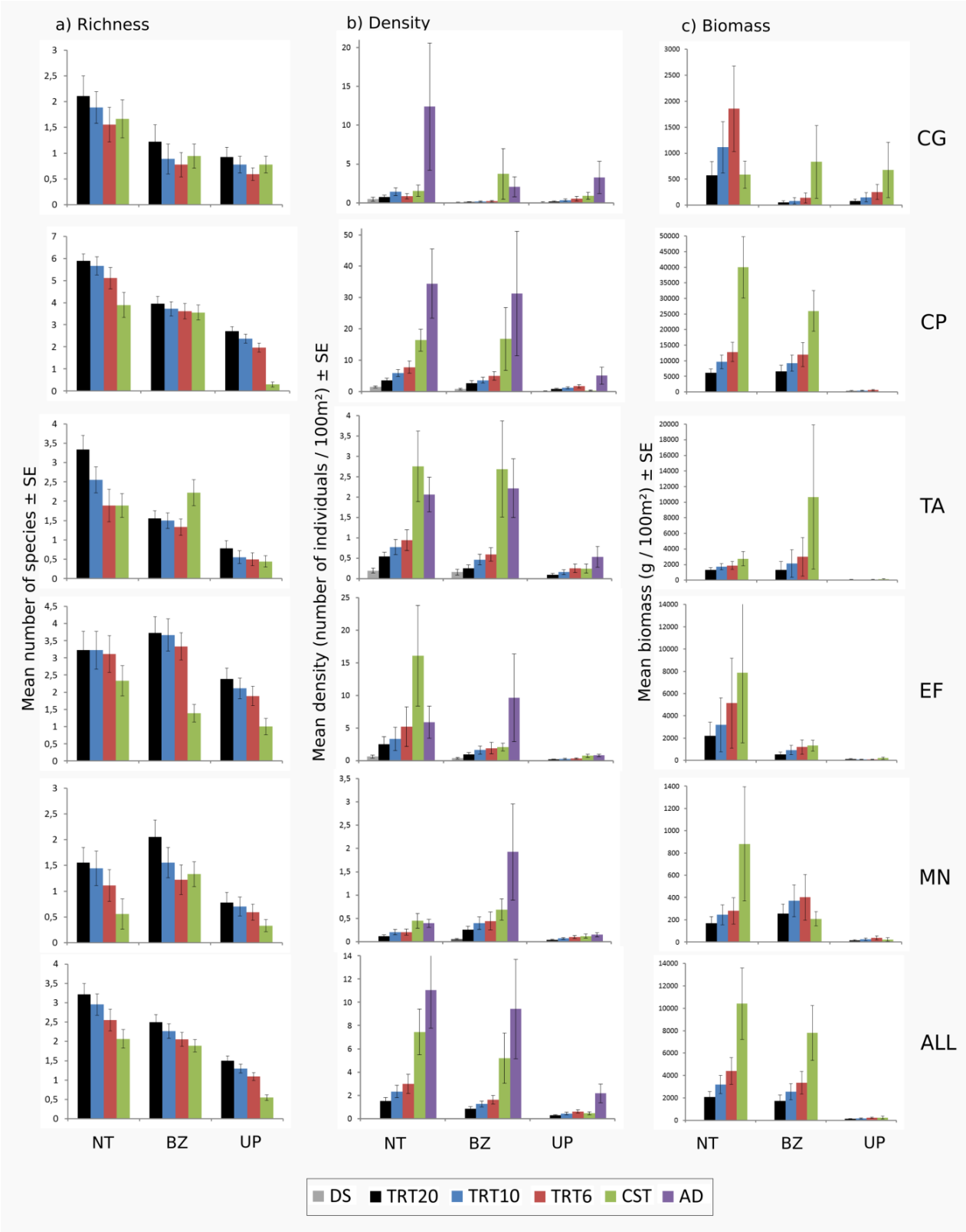


Figure 2. Mean richness (a), density (b) and biomass (c) according to the protection level and the location for the estimators included in the study. NT: no-take zone. BZ: buffer zone. UP: unprotected area. CG: Cabo de Gata. CP: Cabo de Palos. TA: Tabarca. EF: Es Freus. MN: Menorca. ALL: pooled data across MPAs. DS refers to the density value calculated through the distance sampling theory.

3.3. Effect of protection on the density of predatory fish

Density of predatory fish varied according to the Protection Level and the Location considered for all the studied estimators. With all estimators, density was significantly lower in Menorca than the reference level, as did the *AD* estimator for the Es Freus and Tabarca MPAs. Moreover, *ER*, TRT20 and TRT10 found that Cabo de Palos MPA harboured statistically significant higher density, while CST found the opposite pattern for the same MPA (Table 3). According to the protection levels, *AD*, *ER*, TRT20 and TRT10 showed that generally no-take zones harboured greater density of predatory fish (Table 2, Fig. 2b, 3).

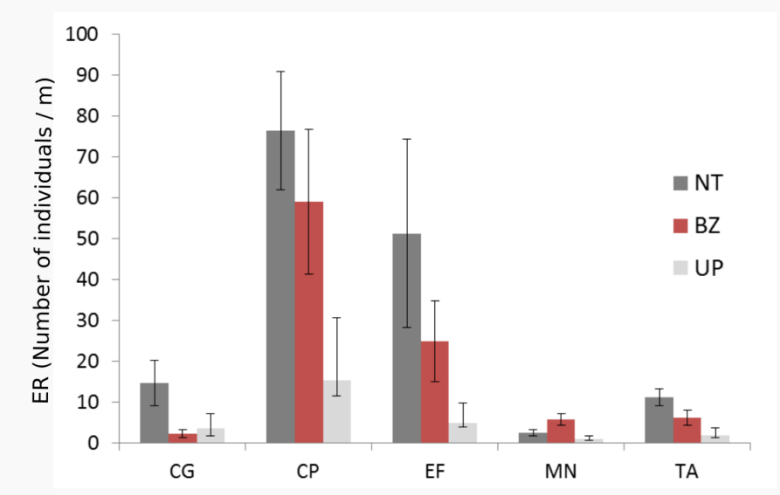


Figure 3. Mean abundance according to the protection level and the location for the ER estimator. NT: no-take zone. BZ: buffer zone. UP: unprotected area. CG: Cabo de Gata. CP: Cabo de Palos. TA: Tabarca. EF: Es Freus. MN: Menorca. Error bars are SE values.

However, when looking at the interactions, *ER*, TRT20, TRT10, TRT6 and CST found that there was significantly greater density in buffer zones of the Cabo de Palos, Es Freus, Menorca and Tabarca MPAs when compared to unprotected areas (except Es Freus for the CST; Table 2). With *AD*, though, we found a greater density both in the no-take and buffer zones of Es Freus, as well as CST did for the no-take of Cabo de Palos MPA (Table 2). The dispersion model showed greater overdispersion in all MPAs and the no-take zone with all the estimators, except the Es Freus MPA when the *ER*

was considered (Table 2). However, the zero-inflation model did not vary according to the factors studied, which means that the proportion of zeros is equivalent among Locations and Protection Levels. Marginal R^2 were around 39–43% for all the estimators considered.

Table 2. Results of the GLMMs for the estimators applied (*ER*, *AD*, TRT20, TRT10, TRT6 and CST) showing the variables explaining the density response variable. Models excluded by AIC are not shown in the table.

	ER			*AD*			TRT20		
Random effects									
Parameter	Variance	SD		Variance	SD		Variance	SD	
ST	0.19	0.43		0.30	0.53		<0.001	<0.001	
Conditional model									
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-3.46	0.43	**<0.001**	-3.13	0.51	**<0.001**	-6.39	0.43	**<0.001**
LOC CP	1.51	0.49	**0.00**	0.23	0.59	0.70	1.45	0.47	**0.00**
LOC EF	0.47	0.58	0.41	-1.60	0.68	**0.02**	0.24	0.55	0.66
LOC MN	-1.40	0.52	**0.01**	-2.76	0.62	**<0.001**	-1.47	0.52	**0.01**
LOC TA	-0.62	0.55	0.26	-1.55	0.65	**0.02**	-0.64	0.53	0.23
PL BZ	-0.40	0.64	0.53	-0.57	0.84	0.50	-0.49	0.65	0.45
PL NT	1.57	0.66	**0.02**	2.07	0.90	**0.02**	1.49	0.64	**0.02**
LOCCP: PLBZ	1.46	0.73	**0.05**	1.56	1.09	0.11	1.47	0.73	**0.05**
LOCEF: PLBZ	1.90	0.83	**0.02**	3.51	0.99	**0.00**	1.93	0.81	**0.02**
LOCMN: PLBZ	2.20	0.76	**0.00**	1.91	1.00	0.06	2.24	0.79	**0.01**
LOCTA: PLBZ	1.56	0.78	**0.05**	1.66	1.06	0.10	1.52	0.78	**0.05**
LOCCP: PLNT	0.11	0.77	0.89	-0.27	1.19	0.80	0.12	0.71	0.87
LOCEF: PLNT	0.71	0.88	0.42	3.04	1.21	**0.01**	1.57	0.86	0.51
LOCMN: PLNT	-0.53	0.82	0.52	-1.72	1.07	0.11	-0.44	0.79	0.57
LOCTA: PLNT	0.30	0.82	0.71	-1.30	1.06	0.22	0.32	0.76	0.68
Zero-inflation model									
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-4.23	1.30	**0.00**	-20.85	3293.04	1.00	-4.46	1.74	**0.01**
Dispersion model									
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-1.20	0.29	**<0.001**	-1.5	0.25	**<0.001**	-1.34	0.27	**<0.001**
LOC CP	1.48	0.34	**<0.001**	1.2	0.29	**<0.001**	1.53	0.33	**<0.001**
LOC EF	0.66	0.37	0.07	0.7	0.31	**0.02**	0.85	0.36	**0.02**
LOC MN	1.65	0.58	**0.00**	1.7	0.40	**<0.001**	1.35	0.53	**0.00**
LOC TA	1.41	0.50	**0.01**	1.8	0.44	**<0.001**	1.41	0.44	**<0.001**
PL BZ	0.21	0.32	0.51	-0.2	0.27	0.41	0.06	0.30	0.85
PL NT	0.83	0.36	**0.02**	0.3	0.30	0.37	0.86	0.35	**0.01**
AIC	1540.01			1633.52			1501.11		
Marginal R^2	0.49			0.54			0.47		

Table 2. Cont.

	TRT10			TRT6			CST		
Random effects									
Parameter	Variance	SD		Variance	SD		Variance	SD	
ST	0.23	0.48		0.12	0.35		0.33	0.57	
Conditional model									
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-5.78	0.5	**<0.001**	-5.34	0.48	**<0.001**	-5.10	0.41	**<0.001**
LOC CP	1.29	0.6	**0.02**	0.87	0.52	0.09	-1.13	0.56	**0.04**
LOC EF	-0.20	0.6	0.75	-0.40	0.58	0.49	0.17	0.62	0.79
LOC MN	-1.60	0.6	**0.01**	-1.63	0.59	**0.01**	-1.78	0.60	**0.01**
LOC TA	-0.75	0.6	0.23	-0.70	0.62	0.26	-1.00	0.65	0.13
PL BZ	-0.73	0.7	0.31	-0.87	0.69	0.20	-0.27	0.60	0.65
PL NT	1.56	0.7	**0.02**	0.89	0.71	0.39	0.83	0.62	0.18
LOCCP: PLBZ	1.70	0.8	**0.04**	0.61	0.77	**0.01**	3.70	0.78	**<0.001**
LOCEF: PLBZ	2.11	0.9	**0.02**	2.13	0.82	**0.01**	1.32	0.86	0.13
LOCMN: PLBZ	2.29	0.9	**0.01**	2.10	0.85	**0.01**	2.00	0.83	**0.02**
LOCTA: PLBZ	1.85	0.9	**0.04**	1.80	0.86	**0.04**	2.57	0.89	**0.01**
LOCCP: PLNT	0.06	0.8	0.94	1.07	0.80	0.18	3.64	0.83	**<0.001**
LOCEF: PLNT	0.02	0.9	0.99	1.25	0.92	0.17	0.75	0.95	0.44
LOCMN: PLNT	-0.47	0.9	0.59	0.14	0.92	0.90	0.55	0.91	0.55
LOCTA: PLNT	0.01	0.9	0.99	0.75	0.91	0.41	1.54	0.93	0.10
Zero-inflation model									
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-3.78	1.29	**0.00**	-3.31	1.05	**0.00**	-20.58	4664.68	1.00
Dispersion model									
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-1.47	0.31	**<0.001**	-1.44	0.30	**<0.001**	-0.59	0.45	0.20
LOC CP	1.63	0.37	**<0.001**	0.68	0.38	**<0.001**	0.50	0.52	0.34
LOC EF	1.04	0.43	**0.02**	1.34	0.46	**0.00**	-0.16	0.49	0.75
LOC MN	1.46	0.63	**0.02**	1.08	0.52	**0.04**	0.90	0.89	0.31
LOC TA	1.39	0.50	**0.01**	1.06	0.51	**0.04**	-0.02	0.52	0.98
PL BZ	0.30	0.34	0.37	0.27	0.33	0.42	0.31	0.46	0.50
PL NT	1.28	0.42	**0.00**	0.83	0.40	**0.04**	1.01	0.50	**0.04**
AIC	1382.93			1213.52			1050.44		
Marginal R^2	0.41			0.39			0.54		

LOC: location. CP: Cabo de Palos. EF: Es Freus. MN: Menorca. TA: Tabarca. PL: protection level. BZ: buffer zone. NT: no-take zone. The final models were: Abundance Estimator ~ ZN * PL + ZN + PL + offset(log(area transect) + (1 | ST). The estimate (including the sign), standard error and p-value of the parameters are shown for the conditional, zero-inflated and dispersion models, as well as the variance and standard deviation of the random effects model.

Table 3. Results of the GLMMs for the estimators applied (TRT20, TRT10, TRT6 and CST) showing the variables explaining the biomass response variable. Models excluded by AIC are not shown in the table.

	TRT20			TRT10			TRT6			CST		
Random effects												
Parameter	Variance	SD		Variance	SD		Variance	SD		Variance	SD	
ST	0.28	0.53		0.44	0.66		0.48	0.70		0.47	0.69	
Conditional model												
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	0.15	0.45	0.74	0.59	0.44	0.18	1.05	0.44	**0.02**	-0.05	0.53	0.93
LOC CP	1.04	0.52	**0.05**	0.86	0.53	0.10	0.72	0.54	0.18	-0.44	0.86	0.61
LOC EF	-0.02	0.56	0.98	-0.65	0.59	0.27	-0.96	0.59	0.10	-0.50	0.70	0.47
LOC MN	-1.33	0.60	**0.03**	-1.15	0.62	0.06	-1.10	0.63	0.08	-1.79	0.81	0.03
LOC TA	-0.18	0.63	0.77	-0.62	0.65	0.34	-0.59	0.66	0.37	-0.29	0.81	0.73
PL BZ	-0.23	0.63	0.71	-0.60	0.70	0.39	-0.54	0.72	0.45	-0.19	0.75	0.80
PL NT	1.49	0.62	**0.02**	1.69	0.64	**0.01**	1.73	0.65	**0.01**	0.29	0.81	0.72
LOCCP: PLBZ	2.73	0.78	**<0.001**	3.34	0.86	**<0.001**	3.17	0.89	**<0.001**	4.22	1.12	**<0.001**
LOCEF: PLBZ	1.72	0.81	**0.03**	2.83	0.89	**0.00**	2.83	0.92	**0.00**	1.82	1.01	0.07
LOCMN: PLBZ	2.29	0.84	**0.01**	2.47	0.92	**0.01**	2.17	0.96	**0.02**	1.44	1.10	0.19
LOCTA: PLBZ	1.00	0.86	0.25	2.00	0.93	**0.03**	1.98	0.98	**0.04**	1.65	1.09	0.13
LOCCP: PLNT	1.46	0.79	0.06	1.39	0.84	0.10	1.25	0.86	0.14	4.46	1.18	**<0.001**
LOCEF: PLNT	0.78	0.85	0.35	0.19	0.91	0.84	0.34	0.92	0.72	2.25	1.13	**0.05**
LOCMN: PLNT	0.38	0.86	0.66	0.07	0.92	0.94	-0.07	0.96	0.94	2.47	1.21	**0.04**
LOCTA: PLNT	1.08	0.87	0.22	1.16	0.92	0.20	1.01	0.95	0.29	1.61	1.15	0.16
Zero-inflation model												
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	0.44	0.33	0.18	0.49	0.32	0.13	0.42	0.32	0.19	0.67	0.35	0.05
LOC CP	-3.26	0.79	**<0.001**	-2.90	0.67	**<0.001**	-2.30	0.56	**<0.001**	-0.09	0.46	0.84
LOC EF	-1.95	0.57	**<0.001**	-1.45	0.49	**0.00**	-1.43	0.49	**0.00**	-0.46	0.51	0.38
LOC MN	-0.34	0.41	0.41	-0.08	0.41	0.84	0.16	0.40	0.69	0.93	0.48	0.05
LOC TA	-0.80	0.46	0.08	-0.76	0.45	0.09	-0.21	0.43	0.62	-0.01	0.50	0.98
PL BZ	-0.92	0.36	**0.01**	-0.84	0.34	**0.01**	-0.80	0.33	**0.01**	-1.90	0.36	**<0.001**
PL NT	-1.95	0.58	**<0.001**	-1.87	0.53	**<0.001**	-1.45	0.46	**0.00**	-2.73	0.51	**<0.001**
Dispersion model												
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-0.16	0.18	0.36	0.03	0.19	0.90	0.07	0.20	0.71	-0.10	0.32	0.77
PL BZ	0.10	0.24	0.67	0.00	0.26	0.99	-0.16	0.27	0.54	-0.50	0.38	0.20
PL NT	0.52	0.28	0.07	0.60	0.31	**0.05**	0.62	0.33	0.06	-0.15	0.39	0.71
AIC	3918.71			3672.23			3445.32			2442.64		
Marginal R^2	0.64			0.64			0.61			0.65		

LOC: location. CP: Cabo de Palos. EF: Es Freus. MN: Menorca. TA: Tabarca. PL: protection level. BZ: buffer zone. NT: no-take zone. The final models were: biomass Estimator ~ ZN * PL + ZN + PL + offset(log(area transect) + (1 | ST). The estimate (including the sign), standard error and p-value of the parameters are shown for the conditional, zero-inflated and dispersion models, as well as the variance and standard deviation of the random effects model.

Mean detection distance was similar among the species considered, and values varied between 1 and 6 m from the observation line (Appendix C). However, this parameter tended to increase as the level of anthropogenic disturbance augmented (i.e. from no-take zones to unprotected areas; no-take = 3.12 ± 1.11; buffer = 3.20 ± 0.39; unprotected = 3.91 ± 0.31 m; mean values across species ± SE), what was more evident for the species *E. costae* (no-take = 2.79 ± 0.92; buffer = 3.72 ± 0.36; unprotected = 4.5 ± 0.29 m; mean ± SE) and *M. rubra* (no-take = 3.03 ± 0.90; buffer = 3.48 ± 0.39; unprotected = 6.00 ± 0.42 m; mean ± SE).

3.4. Effect of protection on the biomass of predatory fish

Biomass of predatory fish was significantly greater in no-take zones than in unprotected areas for the TRT20, TRT10 and TRT6 estimators. Moreover, the TRT20 found that Cabo de Palos MPA reached the greatest biomass of predators while Menorca had the opposite trend (Table 3, Fig. 2c).

Furthermore, TRT20, TRT10 and TRT6 found a positive and significant interaction between Cabo de Palos, Es Freus and Tabarca and the buffer protection level, while CST found positive and significant values of biomass in the no-take and buffer zones of Cabo de Palos, and the no-take of Es Freus and Menorca MPAs (Table 3). In this case, the zero-inflation model varied according to the location and protection level factors, and it was significantly lower for the Cabo de Palos and Es Freus MPAs and both the no-take and buffer zones for most estimators. The dispersion models were only significant for the no-take zone when the TRT10 was considered. Marginal R^2 were between 61 – 65 % for all estimators (Table 3).

4. Discussion

Understanding the best methodological approaches to evaluate MPA performance is of great interest for a correct assessment of protection, particularly when focusing on vulnerable and valuable species. Moreover, determining the effects of both no-take zones and buffer zones in the Mediterranean Sea, where the human population of the surrounding countries is growing fastly (UNEP/MAP 2012) and many livelihoods are

associated to the sea, is essential to evaluate the potential conservation effects of multiple use areas while allowing a certain level of human activity. Our results showed that mean values of density, biomass and richness differed among estimators, so that those covering larger areas yielded higher values of species richness for all MPAs and protection levels, and the values diminished as the census methods covered smaller areas (Fig. 1a). Similar results have been previously found when comparing methodologies; for instance, Thanopoulou *et al.* (2012) found significantly higher mean richness of reef fishes when sampling was done through line transects combined with DS than with CST. Moreover, Loiseau *et al.* (2016) found greater richness estimates when increasing both length and width of transects. This goes in concordance with the well-established species-area relationship (SAR), which states that an increase in the sample area would lead to higher species richness because of an increase in habitat heterogeneity, among other underlying processes (Kallimanis *et al.* 2008; Scheiner *et al*. 2011). However, the method *per se* may be accounting for the increased richness, as methods that use "first contact" are more likely to record fish that may respond to diver's presence than belt transects (Beck *et al.* 2014). Moreover, in the study of Loiseau *et al.* (2016) the effect of varying dimensions was stronger for changes in length than width, and even showed how for a same area covered in the sample, in longer transects richness was significantly higher than in shorter and wider ones. This was explained by the fact that the observer swims all along the transect (whatever the length is) in which detectability is complete, while it may decrease rapidly with increasing widths (Kulbicki *et al.* 2010, Bozec *et al.* 2011, Loiseau *et al.* 2016).

On the other hand, values of density and biomass increased as the area covered by the estimators decreased (Fig. 1b, c), being much greater for the *AD* and CST estimators (the first only in the case of density) and lower for the DS and TRT20. *AD* does not take into account the shape of the detectability curve (as opposed to DS). However, *AD* has been reported to give similar estimates than DS (Kulbicki & Sarramégna 1999), probably because the distances estimated in that study were large. However, in cases in which fish are recorded at small distances, as in our case (i.e. mean distance of the species among 1 and 6 m from the line; Appendix C) the area of

the transects becomes very small (i.e. total average distance 3.66 m ± 0.09 m SE) and the density goes overestimated.

Previous studies found that density estimates obtained with line transects combined with DS were higher than those obtained with CST (Kulbicki & Sarramégna 1999; Thanopoulou *et al.* 2012), and hypothesized that DS would lead to greater density estimates because it takes into account animal detectability and behaviour (e.g. by including species with shy behaviour). However, here we found the opposite pattern: our density estimates made through CST were much higher than those obtained by using DS or TRT methods. Biases associated with CST have been previously reviewed. For instance, Ward-Paige *et al.* (2010), through a simulation model, found that counts using belt transects and stationary-points are overestimated when non-instantaneous census (i.e. counting animals that enter the survey area after the survey has started) are performed, and showed how biases increased with fish speed, although slow moving fish were also overestimated. In fact, calculations applied by Ward-Paige *et al.* (2010) to the results of Sandin *et al.* (2008), which supported the idea of the inverted trophic pyramid in Kingman and Palmyra, were down-sized by two orders of magnitude lower when correcting for the detected bias. In addition, this overestimation was empirically demonstrated by Bradley *et al.* (2017) to be one order of magnitude lower through mark-recapture and acoustic-tracking methods.

Another bias may be related to the observers' tendency to include individuals that are at the edge but outside the sampling area, which has proportionally greater impact as the census area diminishes. The average distance from the diver of the individuals detected in the study was 3.66 m (± 0.09 m SE), which is further than the limit of the CST width (2.5. m); thus, although it is possible that increasing transect areas may have reduced the density estimates as a "dilution effect" (i.e. area increasing more than the number of individuals recorded, which leads to lower density estimates), if the purpose of the study is to have a more accurate estimate of the real values of density and biomass, those methods surveying a larger area would lead to more realistic estimates of fish density and biomass (Prato *et al.* 2017, Irigoyen *et al.* 2018).

The lower density found with the estimators covering larger areas may also be partially explained by a "habitat effect" (García-Charton *et al.* 2004), derived from the generally complex and steep topography of sites at which transects were performed in our study. Wider UVCs include sightings of fish from a wide depth range because it incorporates shallow areas as well as deeper ones due to the narrow and cliffy nature of the rocky reefs, and frequently the deeper and/or shallower areas included other habitat types, such as soft bottoms and seagrass meadows (García-Charton & Pérez-Ruzafa 1998, 2001). This has direct consequences, as the abundance of rocky dweller predatory fish species like groupers is generally lower in both abovementioned habitats.

Therefore, those methods covering larger areas led to higher number of species, as well as the inclusion of more individuals, resulting in more accurate and reliable estimates than methods covering smaller areas. This is supported in our data by the fact that average detection distance increases as the level of protection decreased (as a proxy for the level of human disturbance), especially for some species (*E. costae*, *M. rubra*), thus compromising the reliability of the density and biomass estimates made with CST in unprotected sites. This influence of medium and large commercial fish species behaviour has been previously signalled (Kulbicki & Sarramégna 1991, Irigoyen *et al.* 2018). In this sense, the DS was the most reliable method, as it takes the detectability of the species into account. However, for modelling purposes, achieving 30 records per transect is difficult even in some no-take zones (e.g. Menorca). Nevertheless, if water visibility do not allow for performing DS, any of the TRT will be a solution for increasing the area sampled and performing calculations easily, and especially the TRT20, which allows the detection of most of the species.

Regarding the effectiveness of the MPAs in the conservation of predatory fish, although differences were found according to the estimator considered, it can be sum up that all MPAs, except Menorca, are being ecologically effective. Cabo de Palos and, to a lesser extent, Es Freus, were the MPAs with the greatest fish species richness, density and biomass. Marginal R^2 values show that, in general, the models obtained

explain a remarkable proportion of the observed variability, although other variables not included here might be also responsible for the patterns found.

In addition to fishing pressure, primary production has been proposed as one of the most important factors affecting the dynamics of fish populations in the Mediterranean Sea ecosystem, as it reflects the amount of energy that enters and leaves the ecosystem, and controls food availability and hence fish biomass (Piroddi *et al.* 2017). Here, Menorca was the MPA performing the worst in terms of conserving predatory fish, coinciding with the lowest level of primary productivity (Cardona *et al.* 2007), which may be partly responsible of the pattern found. However, we did not find a response of the other MPAs according to the level of primary productivity, as Cabo de Palos and Es Freus were the MPAs performing better, but these MPAs are not located at any end of the gradient of primary productivity. Therefore, other MPA features and local environmental conditions should be concurrently accounting for the observed patterns.

Many factors have been found to affect the effectiveness of MPAs for the conservation of fish, such as the area of the no-take and the buffer zones, the time elapsed since the protection has been in force, or the level of enforcement. All MPAs included in this study have been protected for long periods (i.e. the number of years between the implementation of the MPA and the study date), from 17 (Menorca) to 31 years (Tabarca). The number of years necessary to detect a response to protection varies with the species considered. For high level predators, that usually have slow growth, large sizes and long lives (Reynolds *et al.* 2005), the effects of protection are expected to be noticed in the long term (from 5 to 20 years; Claudet *et al.* 2008, Guidetti & Sala 2007, Edgar *et al.* 2014, Friedlander *et al.* 2017), thus all MPAs in the study are susceptible to have reached the age to show comparable results.

Moreover, enforcement has been found as a critical factor driving ecological effectiveness (Guidetti *et al.* 2008, Edgar *et al.* 2014, Giakoumi *et al.* 2017, Rojo *et al.* 2019). Although it was previously thought that bigger no-take zones would produce greater benefits (Claudet *et al.* 2008, 2010, Edgar *et al.* 2014, Friedlander *et al.* 2017), it has been recently found that even small but well enforced MPAs are effective for

some commercial fish species and the whole community in the Mediterranean Sea (Giakoumi *et al.* 2017) and for piscivores populations worldwide (Rojo *et al.* 2019). In our study, no-take zones ranged between 78 (Tabarca) and 2310 (Cabo de Gata) hectares, with four out of five no-take zones occupying less than 1000 ha. Cabo de Palos, followed by Tabarca and Es Freus were the MPAs in which there were higher levels of enforcement, measured as the total annual number of days with surveillance and of poaching (following Guidetti *et al.* 2008). Moreover, Menorca was found to have scarce patrol programs, as is the case also in Cabo de Gata (Félix-Hackradt *et al*. 2018), which may explain in part the lack of ecological effects of protection measures in these MPAs.

Importantly, our results show that, when looking at specific MPAs, buffer zones support higher density and biomass of predatory fish compared to unprotected areas. Moreover, mean values appeared to be similar between no-take and buffer zones (even greater, i.e. Menorca; Fig. 2), which may indicate that this partially protected areas are being effective for the conservation of predatory fish. Buffer zones are traditionally seen as less beneficial for the species than no-take zones (Lester & Halpern 2008, Sciberras *et al.* 2013, Giakoumi *et al.* 2017, Sala & Giakoumi 2017), especially when the species being harvested are the same that are protected in no-take areas (Sciberras *et al.* 2013). Some authors even consider that they might reduce the effectiveness of the entire MPA when their sizes are excessively large, as these areas are attractive for local artisanal fishers, thus reducing MPA efficacy (Claudet *et al.* 2008). However, it has been recently found that buffer zones can be ecologically effective when they are well regulated and located adjacent to fully protected areas (Abecasis *et al.* 2015, Zupan *et al.* 2018), as is the case of the MPAs in our study. Buffer zones benefit through spillover from no-take zones, either of adults or by larval dispersion. The fact that they may enhance ecological benefits is especially important in the Mediterranean Sea, where traditionally many livelihoods are linked to the sea (Di Franco *et al.* 2016). The activities allowed in buffer areas are usually small-scale fisheries and recreational diving, the first representing around 80% of the fishing boats in the Mediterranean Sea, hence being an activity of enormous socio-economic importance for the local communities (Maynou *et al.* 2013). Thus, if buffer zones are

ecologically effective, they may help to achieve a win-win scenario in which both fish and fishermen would benefit from protection measures (Dalton 2010).

Particular environmental conditions of each MPA could exert additional influence on the observed values of species richness, density and biomass of predatory fish species (Rojo *et al*. in prep.), such as the differential spatial arrangement and structure of the reef habitat (García-Charton *et al*. 2004), fluctuations in spatial and temporal patterns of reef fish larval dispersal (Calò *et al*. 2013, 2018) and subsequent changes throughout the different early-life history stages of fishes, such as settlement and recruitment (Félix-Hackrad *et al*. 2013), and the contribution of energetic subsidies to the local food web as determinants of the trophic structure (Trebilco *et al.* 2013, Barneche *et al.* 2014).

In conclusion, regarding the methodologies applied, most estimators allow for the detection of the effects of protection on fish assemblages, but they yield slightly different patterns. However, we have shown that those UVC methodologies covering larger areas allowed for a better detection of most of the predatory species studied, and yielded more realistic and accurate estimates for the response variables. Therefore, we recommend to routinely adopt methodologies that include larger sampled areas (and, more specifically, to use TRT+DS or TRT20) when surveying predatory fish populations (for instance to evaluate MPA performance or to measure demographic parameters of the species), and combine them with CST or narrow-width TRT techniques to sample other groups of fishes. On the other hand, we have shown that partially protected areas of the studied MPAs are effective for the conservation of predatory fish species in the Western Mediterranean. Thus, well-managed partially protected areas (in combination with no-take zones) are still to be retained as an important tool to conserve marine resources and protect marine biodiversity. In addition, the variability in the effectiveness of the studied MPAs may be due to both environmental (differences in primary production, habitat structure and 'supply-side' effects) and management factors, namely enforcement level. This can have consequences for the expected recovery of fish populations at a regional scale.

5. Appendices

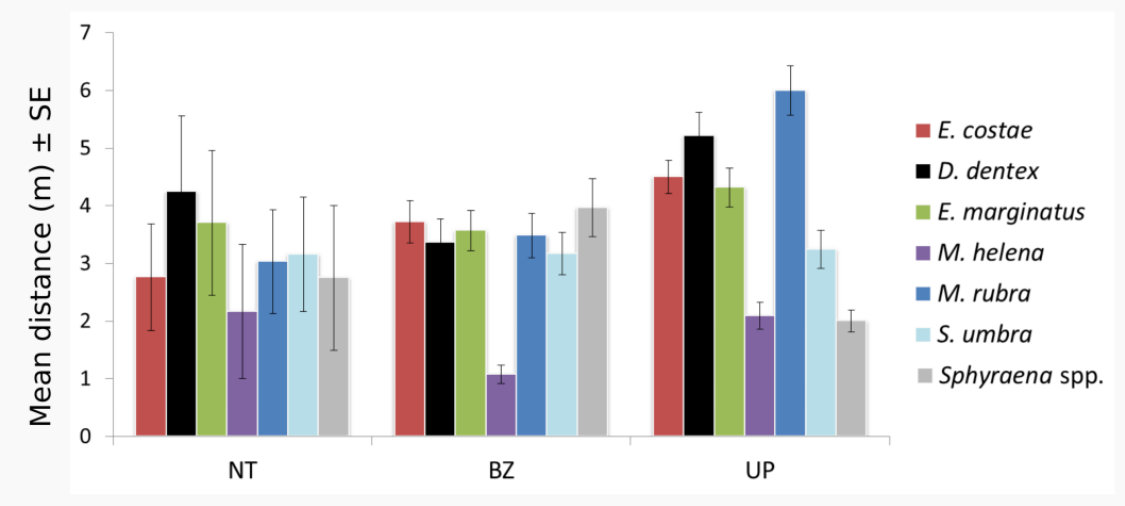
Appendix A. Features characterizing the MPAs included in the study.

MPA	No-take size (ha)	Buffer size (ha)	Year established	Enforcement
Cabo de Gata	2310	10149	1995	low
Cabo de Palos	838	4144	1995	high
Tabarca	78	1322	1986	high
Menorca	403	13314	1999	low
Es Freus	270	1661	1999	medium

Appendix B. Complete set of species recorded in the study, and the percentage occurrence in the transects performed, including the two methodologies TRT+DS and CST. Species selected for the study for being in at least 10 % of the transects are highlighted in bold.

Species	% occurrence
M. aquila	1
S. aurata	6
E. costae	15
D. dentex	28
E. marginatus	39
M. helena	13
M. rubra	10
S. umbra	24
Sphyraena spp.	11
D. labrax	2
S. scrofa	1
S. dumerili	7
E. alletteratus	3
C. crysos	1
T. marmorata	0
E. caninus	0
P. pagrus	0
S. sarda	1

Appendix C. Mean sighting distances of the 7 most abundant species included in the analyses by protection level. Data were polled across locations. NT: no-take zone. BZ: buffer zone. UP: unprotected area.



CHAPTER 4

Habitat selection of predatory fish in Mediterranean protected and unprotected areas

Habitat selection of predatory fish in Mediterranean protected and unprotected areas

1. Introduction

High trophic-level species have traditionally been targeted by fisheries, and are one of the most affected groups in the marine ecosystems (Pauly *et al.* 1998, Myers & Worm 2003), especially in the Mediterranean Sea (Piroddi *et al.* 2017). High-level predators have a strong influence on the structure and functioning of marine communities (Tegner & Dayton 2000, Ritchie & Johnson 2009) and are indicators of the conservation status of the entire ecosystems (Stallings 2009). Thus, effective protection must be provided to ensure the conservation and restoration of their populations.

Marine Protected Areas (hereafter MPAs) have been established as a tool for fisheries management in order to conserve fishing resources, as well as to protect marine biodiversity (Pérez-Ruzafa *et al.* 2017); as such, MPAs are well known to have positive effects on fish populations (Giakoumi *et al.* 2017) - particularly top predators (Guidetti *et al.* 2014, Rojo *et al*. 2019), thus benefiting the fishing activity operating adjacent to the MPA, either by spillover of adults, juveniles or larvae (Di Lorenzo *et al.* 2016), and on the benthic habitats, by improving their quality as a consequence of reduced fishing impacts (Rodwell *et al.* 2003).

Habitat selection in fishes is the result of a combination of external factors, such as environmental conditions, food availability, and shelter (Planque *et al.* 2011), and internal factors, such as population size and density-dependent effects (Aarts *et al.* 2013). When density-dependence modulates habitat selection, fitness in a habitat decreases as density increases (Morris 2003). Thus, increasing abundances may lead to a shift of the species from optimal to marginal habitats due to resource competition (Valvanis *et al.* 2008, Bartolino *et al.* 2011).

Typically, marine fish have multiple life stages, which usually include a dispersive larval phase followed by a settlement and metamorphosis to a benthic immature juvenile and adult phase (Miller & Kendall 2009). Often, the habitat

requirements of the species change throughout their ontogeny, which determines their spatial distribution along their life cycle (Lee *et al.* 2019). In this sense, MPAs must be designed including some or all of the species life stages to provide effective protection (Gailaduk *et al.* 2018). Hence, understanding habitat requirements at each life stage is essential for proper management and protection, especially for populations at risk.

Species Distribution Models (SDMs) represent a useful tool to understand the relationships among species and environmental variables. They allow for statistically associated species occurrence (presence only, presence/absence or abundance) with predictor environmental variables, which are geographically mapped, to understand the variables that correlate to their occurrence and their spatial distribution (Guisan & Zimmermann 2000, Elith & Leathwick 2009). SDMs have been applied with the aim of understanding the niche of the species in an area (Wedding and Yoklavich 2015), their potential distribution under different climatic conditions (Martinez *et al.* 2015, Kotta *et al.* 2019), the potential distribution of invasive species (Mainali *et al.* 2015, Davis 2019) or the best locations for spatial management actions (Zellmer at al. 2019). Moreover, SDMs are widely applied in conservation ecology, and allow for understanding the proportion of suitable habitats protected by conservation measures and the benefit of protected areas on the species (Abecasis *et al.* 2014).

In the marine ecosystems the development of SDMs has appeared during the last decade (e.g. Cañadas *et al.* 2005, Albañez-Lucero & Arreguín-Sánchez *et al.* 2009, Monk *et al.* 2010, Abecasis *et al.* 2014) and is growing in importance, mainly due to the increasing access to multibeam sonar, which provides detailed bathymetry data for the production of digital terrain models and variables derived from topography (Wilson *et al.* 2007). Moreover, the development of new sampling techniques has allowed marine studies to enhance the acquisition of data by using underwater visual census methodologies to gather spatial information by geo-referencing the paths performed during the transects (Lynch *et al.* 2015, Irigoyen *et al.* 2018). Additionally, underwater video camera systems are increasingly being used (Watson *et al.* 2005, Trobbiani *et al.* 2018, Grane-Feliu et al. 2019), thus access to marine information has experienced an important growth in the last years.

Previous studies have attempted to understand the environmental variables that affect the distributions of some teleost high-level predators species in the Mediterranean Sea (such as *Epinephelus marginatus, Epinephelus costae* or *Mycteroperca rubra*; La Mesa *et al.* 2002, García-Charton *et al.* 2004, La Mesa *et al.* 2006, Claudet *et al*. 2011, Reñones *et al.* 2012, Hackradt 2012, Álvarez-Berastegui *et al.* 2018), finding that variables such as depth, rugosity and slope are the ones that contribute the most to explain the distribution of the species. However, to our knowledge, no SDM have previously been performed on these Mediterranean species. The present study aimed at evaluating the distribution of high-level predatory species in several protected and unprotected locations in SW Mediterranean to identify the environmental variables that affect their spatial distribution, so that habitat suitability maps can be built. In the context of MPA design, it is especially important to understand whether the habitats included in the protected area allow the presence of viable populations of focal species. Thus, our objective was to assess whether the MPAs are suitable for high-level predator species and to identify potential new areas for the establishment of other MPAs in the area. Specifically, we performed SDMs in i) the Cabo de Palos- Islas Hormigas marine reserve, which has been established since 1995, and ii) the Cabo Tiñoso marine reserve, which was established in 2016, together with the Cabo Cope unprotected area, with the aim to evaluate habitat selection in areas with different density of reef fish. In each of the areas we evaluated the entire population of the selected species, and distinguished between the immature and the mature individuals separately to identify changes in habitat selection throughout their life cycles. Based on previous studies, we hypothesized that (i) fish will show preferences for rocky habitats with high complexity, (ii) habitat selection will be optimal in areas with lower abundance of fish, and will shift to sub-optimal habitats as density increases, and (iii) habitat selection will show differences between mature and immature individuals. Our results will help to identify the most important variables for the studied species and hence asses the adequacy of the protected areas presently in force and the selection of new appropriate areas for protection.

2. Material and Methods

2.1. Study area

The study was performed in the coast of Murcia (SE Spain), where tThree locations were selected due to their ecological relevance, the Cabo de Palos-Islas Hormigas marine reserve, the Cabo Tiñoso marine reserve, and the unprotected area of Cabo Cope (hereafter CP, CT and CC, respectively; Fig. 1).

The CP MPA was designated in 1995 under fisheries legislation. It has a no-take zone occupying 270 ha around the Hormigas islands, where all activities are banned, except scientific research (if previously authorised). The buffer zone surrounds the no-take zone and occupies 1661 ha, in which recreational diving and small scale fisheries are allowed but strongly regulated. The MPA consists in a rocky coastal area and a series of steep seamounts and islands that continue from the cape towards the north-east.

The CT MPA was established in 2016, also under fisheries legislation, and occupies a coastal stretch of about 15 km in length, from which the cape Tiñoso is the projection into the sea of a coastal high cliff that extends for around 7 km, and the rest is occupied by alluvial coast with some rocky extrusions. The protected area goes from the coast to the –50-m isobath, and cover a surface of 1173 ha; the zonation is established under four different protection levels (A-D cells, Fig. 1), with the activities regulated differently according to the cell: cell B is the no-take zone, where neither fishing nor diving is allowed, in cells A and C recreational diving and artisanal fisheries are allowed but regulated, and in cell D artisanal fisheries are authorised and regulated while recreational fisheries and diving are allowed without restrictions.

CC is an unprotected area located in the southernmost sector of the coast of Murcia. This coastal stretch consists of a medium-to-high cliff interspersed with small beaches of alluvial origin, in which several rocky formations stand out, namely, from west to east, 'Cabeza de Caballo' outcrop, 'Fraile' island and, above all, the cape of Cope, an impressive limestone promontory that plunge into the sea and runs for more

than 3 km. The regional government is planning to establish a new MPA around this area in the next years.

All three areas have similar sea-bottom habitats, which consist of rocky boulders, sand patches and seagrass meadows in the shallower zones, and detrital areas at greater depths. Apart from the rocky areas, which are mostly near the shore, the rest of the seabed is mainly sedimentary.

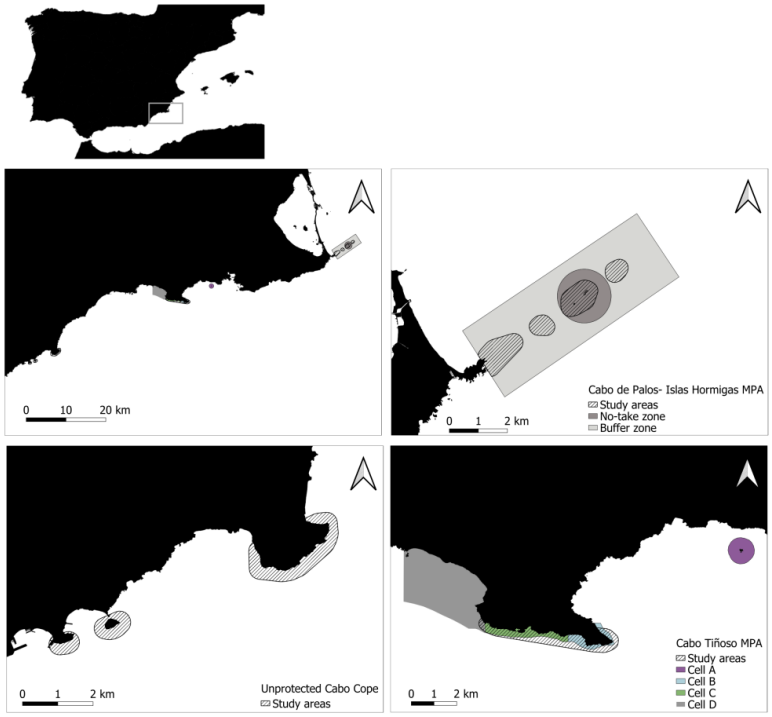


Figure 1. Map showing the location of the three study areas in the coast of Murcia. Protection levels are noted, and selected study areas are highlighted.

The extension of the MPAs and the unprotected area are much greater than the areas in which observations were sighted. Indeed, all areas include a high proportion of sedimentary bottoms, in which individuals were scarce or completely absent. Thus, including the entire areas would have led to strong observation biases and the results would only show a preference of rocky bottoms over sedimentary ones. Hence, in order to better discern among rocky features, we defined an area calculated as a 300-m buffer from the minimum polygon including all the observations in every location, reducing the study area to an area with similar observation probability.

2.2. Species selected and sampling methodology

The study focused on several predatory fish species, namely *Epinephelus marginatus, Epinephelus costae, Mycteroperca rubra, Dentex dentex*, *Sciaena umbra*, *Sphyraena viridensis* and *Muraena helena*. These species are important economic resources in the Mediterranean Sea both for fisheries, both small-scale professional and recreational, and tourism (Coll *et al.* 2004, Briquet-Laugier *et al.* 2007, Lloret *et al.* 2008, Lloret & Riera 2008). Moreover, most of the species are included in some of the IUCN threat categories because of the decline of their populations (IUCN 2017). All species are medium-to-large-sized fish and are among the most benefited by marine protection in the area (García-Charton *et al.* 2018).

The occurrence of these species was recorded by using two different methodologies, underwater visual censuses performed following the tracked roaming transects combined with distance sampling methodology (TRT+DS; Irigoyen *et al.* 2018), and a geo-referenced towed underwater camera system (Trobbiani *et al.* 2018).

In TRT+DS, transects of variable length were performed by two divers following an imaginary line at a constant depth. At the same time, the path was being recorded by a GPS located on a body-board on the surface. Transects lasted 8 minutes on average, and the start/end census points were identified by geo-referencing them with a synchronized clock (see Irigoyen *et al.* 2018 for details). Mean transect length was 110 m (± 2 m SE). Sampling was done through the distance sampling methodology (Buckland *et al.* 2001), indicating the first-sight perpendicular distance of the individuals from both sides of the imaginary line. This method was carried out in the three areas during the summer of 2016, 2017 and 2018.

Additionally, during the summer of 2016 and 2017 and only in CP, sampling was performed by using a towed video camera system, consisting of an underwater camera connected to the boat through a cable, which allowed real-time watching of what was being filmed (Trobbiani *et al.* 2018). Boat trajectories were tracked with a GPS, so synchronizing the camera to the GPS it was possible to locate each observation by its spatial coordinates. With this method, we covered all the rocky areas and some of the adjacent sedimentary zones.

2.3. Ecogeographical variables (EGVs)

We considered several EGVs as explanatory variables, grouping them into two categories: (i) bathymetry and derived variables, extracted from a digital terrain model of the sea bottom, and (ii) variables of the benthic habitat, all at 30-m cell resolution. From the bathymetry, we computed 9 derived variables, which are indicative of seabed morphology and have been identified in other studies as potential predictors of fish species distributions (Monk *et al.* 2010, Biber *et al.* 2013, Abecasis *et al.* 2014, Wedding & Yoklavich 2015, Sánchez-Carnero *et al.* 2016): depth, slope (maximum change in depth between each cell and neighbor cells), orientation (i.e. northness and eastness; deviation of aspect from north and east, respectively), plan, profile and mean curvatures (which are perpendicular, parallel and mean to the direction of maximum slope, respectively), terrain ruggedness index (topographic heterogeneity; hereafter TRI), rugosity, and bathymetry position index (elevation relative to the overall landscape, hereafter BPI). For its part, benthic habitat was characterised by the categorical variable habitat type, which accounts for both the size of grain (rock, sand, pebblles and mud and the biota living over the bottom (seagrasses, algae, molluscs, etc.) (information taken from the public repository of the Ministry for the Ecolgical Transition www.miteco.gob.es) (see Appendix A for a list of the habitats present in each study area).

Since habitat selection may be influenced by density-dependent processes (Valvanis *et al.* 2008), data of CT and CC were grouped together and treated jointly as a single study area (and hereafter called CTCC) because the abundance of fishes has been identified to be significantly higher in the CP MPA than in the CT MPA or CC area (García-Charton *et al.* 2016), and there were no significant differences between the mean of the environmental variables (t.test = 0.927, P = 0.38) nor the standard deviation (t.test = -0.739, P = 0.48) of these two locations. The lack of reserve effects in CT is likely due to the short time elapsed since the inception of protection measures in this location (2 years at the moment of sampling). Table 1 shows the range of each variable in CP and CTCC and their mean values.

2.4. Species Distribution Models (SDMs)

We performed SDMs to understand the environmental variables that affect the distribution of the selected species, as well as to build the habitat-suitability maps. We performed three analyses in each of the locations (CP and CTCC), one considering all the individuals of the species, one analysis taking into account separately the immature individuals, and the last one accounting only for the mature individuals. The first analysis included data recorded with both census methodologies (UVCs using TRT+DS, and towed video) in CP and only UVCs using TRT+DS in CT and CC, while the immature and mature analyses were performed only with data from UVCs, as fish size was not possible to be identified through the towed video camera system methodology.

Table 1. Minimum and maximum range and mean values for the EGVs in the two study areas, CP (Cabo de Palos-Islas Hormigas marine reserve) and CTCC (Cabo Tiñoso marine reserve and the unprotected Cabo Cope). BPI: bathymetry position index. TRI: terrain ruggedness index.

	CP			CTCC		
	min	max	mean	min	max	mean
bathymetry	-79.170	-6.325	-40.393	-74.332	-5.285	-35.885
BPI	-0.184	0.381	0.000	-0.322	0.279	0.001
curvatures	-1.444	2.979	0.004	-6.625	5.509	0.004
plan curv.	-0.894	1.568	0.024	-2.652	2.265	0.003
profile curv.	-1.533	1.158	0.020	-3.244	3.973	-0.001
eastness	-1.000	1.000	0.344	-0.854	1.000	0.245
northness	-1.000	1.000	-0.033	-1.000	0.742	-0.719
rugosity	0.015	8.191	0.805	0.182	1.930	1.122
slope	0.046	31.972	3.555	0.372	9.873	5.205
TRI	0.018	7.431	0.775	0.180	2.025	1.126

The criterion for classifying in immature and mature individuals was their size at first maturity, which is defined as the size at which 50% of a population has reached sexual maturity for the first time (Tsikliras & Stergiou 2013). Size at first maturity was 35 cm for *E. costae* (Froese & Pauly 2017), 50 cm for *E. marginatus* (Marino *et al.* 2001, Reñones *et al.* 2010), 33 cm for *D. dentex* (Cetinic´ *et al.* 2002, Grau *et al.* 2016, Froese & Pauly 2017), 30 cm for *S. umbra* (La Mesa *et al.* 2008, Grau *et al.* 2009, Froese & Pauly 2017), 25 cm for *M. rubra* (Aronov & Goren, 2008, Froese & Pauly 2017) and 60 cm for *S. viridensis* (Bourehail *et al.* 2010). It was not possible to differentiate between

immatures and matures in the case of *M. helena* because data on fish length was not available for this species, as it lives mostly inside cracks and fissures in the rock.

2.4.1. Ecological niche-factor analysis (ENFA)

We used ecological niche-factor analysis (ENFA; Hirzel *et al.* 2001, 2002), which is a presence-only multivariate approach that compares the distribution of the EGVs in the localities where the species were observed to the global distribution of the EGVs in the whole study area. The analysis assumes the EGVs are normally distributed in the study area. Hence, a Box-Cox transformation was applied to improve their Gaussianity. Once achieved a Gaussian-like symmetric distribution, normalized marginalities can be compared with Gaussian distribution percentiles to identify common or rare values.

The difference between the mean values of the localities where focal species have been observed (Xs) to the mean values of the area (Xt) is expressed as the species marginality (M), so that the more different those means are, the more marginal the species is. Marginality is expressed as $M = \frac{\sqrt{\sum_{j=1} m_i^2}}{1.96}$, with $m_i = \frac{|Xt - Xs|}{1.96 \cdot SDt}$, being SDt the standard deviation of the EGVs in the total area.

When the difference concerns the variances instead of the means, we refer to the species specialization, which indicates the range of the EGV values in which the species are present compared to the global variances. Thus, the smaller the range, the more specialized the species. Hence, species specialization is defined as $S^2 = \sum_i s_i^2$, where $s_i^2 = \frac{average[U_i \cdot (Xt - O)]^2}{average[U_i \cdot (Xs - M)]^2} = max$, being U_i each of the specialization axes, $M = average(Xs)$, and $O = average(Xt)$. Specialization was calculated by retaining only the 3 largest specialization axes.

A marginality greater than |1| is indicative that the species was marginal for the variable. Regarding specialization, a value ≤1 indicates that the species could choose any of the EGV values in the study area along that axis, while a value ≥1 means that the species was very specialized and was only tolerant to a small range of EGV values.

2.4.2. Habitat suitability index

The habitat suitability index (HSI) was estimated by the Mahalanobis distance from each point to the species habitat center (Calenge *et al.* 2008). HSI is calculated using ENFA marginality and specialization axes. HSI in a pixel is defined as the probability of finding a less suitable point (i.e. with a larger Mahalanobis distance to the center of the species EGV space) than P in the whole study area. Thus, $HSI(P)$ is constrained to values between 0 and 1 (Hirzel *et al.* 2002). HSI is computed ordering the Mahalanobis distances to the species origin of all the N pixels in the study area, from smaller to larger, and then using the ranked position $n(P)$ of pixel P to obtain $HSI(P) = 1 - \frac{n(P)}{N}$.

HSI validation was done through the Boyce index (Boyce *et al.* 2002, Galparsoro *et al.* 2009, Sánchez-Carnero *et al.* 2016), which is based on the Spearman rank correlation among HSI and the number of observations per interval of HSI values. Boyce index was cross-validated by extracting a random sample of 10% of the sites and calculating the Boyce index with those sites not used in the calculation (Sánchez-Carnero *et al.* 2016).

All analyses were performed with R (R Development Core Team, 2015) and adehabitatHS package (Calenge 2006), with some adaptations to include observation weighting (instead of only presence) and compute habitat suitability according to ENFA, following Sánchez-Carnero *et al.* (2016).

3. Results

3.1. Cabo de Palos - Islas Hormigas marine reserve

3.1.1. All individuals

Boyce indices revealed a good fit for all models (> 0.9) except for *M. helena* (Boyce index = 0.4). All species showed high marginalities (larger than 4) and similar values among them (range 4.6 to 6.1). All the EGVs included in the analysis, except

orientation, contributed to species' marginalities (Table 2). Moreover, all species showed preferences for habitat 6 ("photophilic algae + red algae - urchins + pre-coral + caves - overhangs").

Results show a high specialization (values generally above 200) for all species. *M. helena* was the species with the highest specialization, between 4 and 10 times greater than the other studied species. Most species showed dependence on bathymetry and habitat complexity (characterized by TRI, BPI and rugosity; Table 2).

HS maps were similar among species. The shallowest areas of seamounts and islands and the furthest area from the coast were the zones with the highest HSI. For *S. umbra*, though, the most coastal area showed a higher HSI (Fig. 2).

3.1.2 Immature individuals

In addition to *M. helena*, it was not possible to analyse *M. rubra* because of the low number of pixels with observations of immature individuals of this species (Table 3). Models showed a good fit for all species (Boyce indices > 0.7) except *E. costae* (Boyce index = 0.48). Marginality was high for all species, being greatest for *E. marginatus* and *S. viridensis* (values > 5) and lowest for *E. costae* (2.7). All EGVs, except orientation, contributed to *D. dentex*, *E. marginatus*, *S. umbra* and *S. viridensis* marginalities. This pattern was different for *E. costae*, for which marginality was mainly determined by bathymetry, mean curvature and BPI (Table 3). All species showed preferences for habitat 6 ("photophilic algae + red algae - urchins + pre-coral + caves - overhangs").

The studied species showed high specialization values (above 600). *S. umbra* had the greatest specialization (among 10 and 25 times higher than the other species) and *E. marginatus* had the lowest values. All species showed a greater contribution of bathymetry and habitat complexity to specialization, although the variables accounting for the habitat complexity slightly differed according to the species (Table 3). Maps showed a greater HS in the shallower seamounts and the coastal area for all species (Fig. 3).

Table 2. ENFA results, specifying A) Boyce index, B) the number of pixels with observations for each species, C) results of the total marginality and the contribution of the EGVs to marginality and D) total specialization and the contribution of the EGVs to specialization for each of the studied species in CP when considering all individuals together.

	E. costae	*D. dentex*	*E. marginatus*	*M. helena*	*M. rubra*	*S. umbra*	*S. viridensis*
A) Boyce index	1.00	0.99	0.99	0.36	0.98	0.94	0.99
Boyce I. 10%	0.97 ± 0.02	0.96 ± 0.02	0.98 ± 0.01	0.42 ± 0.36	0.95 ± 0.03	0.95 ± 0.03	0.93 ± 0.06
B) Nº Pixels	76	74	108	18	56	43	142
C) Marginality	5.30	6.11	5.79	5.44	5.30	4.62	4.72
bathymetry	**1.16**	**1.17**	**1.18**	**1.16**	**1.20**	**1.25**	**1.08**
BPI	**2.56**	**2.86**	**2.78**	**2.30**	**2.36**	**1.95**	**2.21**
curvature	**2.45**	**2.76**	**2.71**	**2.22**	**2.24**	**1.82**	**2.11**
plan curv.	**2.21**	**2.38**	**2.23**	**2.10**	**2.41**	**1.28**	**2.05**
profile curv.	**-1.99**	**-2.43**	**-2.41**	**-1.69**	**-1.50**	**-1.72**	**-1.58**
eastness	-0.46	-0.57	-0.53	-0.95	-0.34	-0.63	-0.65
northness	-0.15	0.14	0.01	0.51	-0.19	0.27	0.27
rugosity	**1.29**	**1.67**	**1.40**	**1.80**	**1.62**	**1.59**	**1.22**
slope	**1.30**	**1.64**	**1.40**	**1.78**	**1.62**	**1.59**	**1.22**
TRI	**1.35**	**1.67**	**1.44**	**1.80**	**1.62**	**1.60**	**1.27**
habitat 6	**5.39**	**9.00**	**6.58**	**8.46**	**6.72**	**8.08**	**5.55**
D) Specialization	326.98	291.87	362.15	2165.00	575.50	406.08	184.80
bathymetry	**4.0E-02**	**2.6E-02**	**3.5E-02**	3.1E-04	**1.4E-02**	9.3E-03	**2.4E-02**
BPI	2.2E-04	2.4E-04	3.0E-04	2.0E-05	4.9E-04	1.1E-03	1.3E-03
curvatures	4.8E-06	1.1E-03	5.6E-04	3.0E-03	1.0E-05	2.2E-03	1.4E-04
plan curv.	5.8E-05	6.7E-04	5.0E-05	8.8E-04	1.7E-04	5.6E-05	8.9E-04
profile curv.	8.7E-05	9.6E-04	7.2E-06	1.1E-03	6.0E-05	1.4E-04	2.7E-05
eastness	6.2E-06	2.5E-04	3.6E-06	1.9E-04	9.7E-07	1.5E-03	1.3E-03
northness	2.5E-06	2.5E-05	9.4E-06	2.0E-06	3.0E-05	3.9E-04	3.1E-05
rugosity	7.9E-04	**1.8E-02**	9.8E-03	6.8E-04	**3.1E-02**	4.4E-03	1.7E-03
slope	8.0E-03	**6.0E-02**	**3.6E-02**	**4.7E-01**	**2.1E-01**	**1.6E-01**	**1.2E-02**
TRI	**2.2E-02**	**4.8E-02**	**2.4E-02**	**5.0E-01**	**1.3E-01**	**1.8E-01**	**3.2E-02**

BPI: bathymetry position index. TRI: terrain ruggedness index. Habitat 6: photophilic algae + red algae - urchins + pre-coral + caves – overhangs. Only significant habitat categories are shown in the table. The variables significantly contributing to marginality and specialization are highlighted in bold.

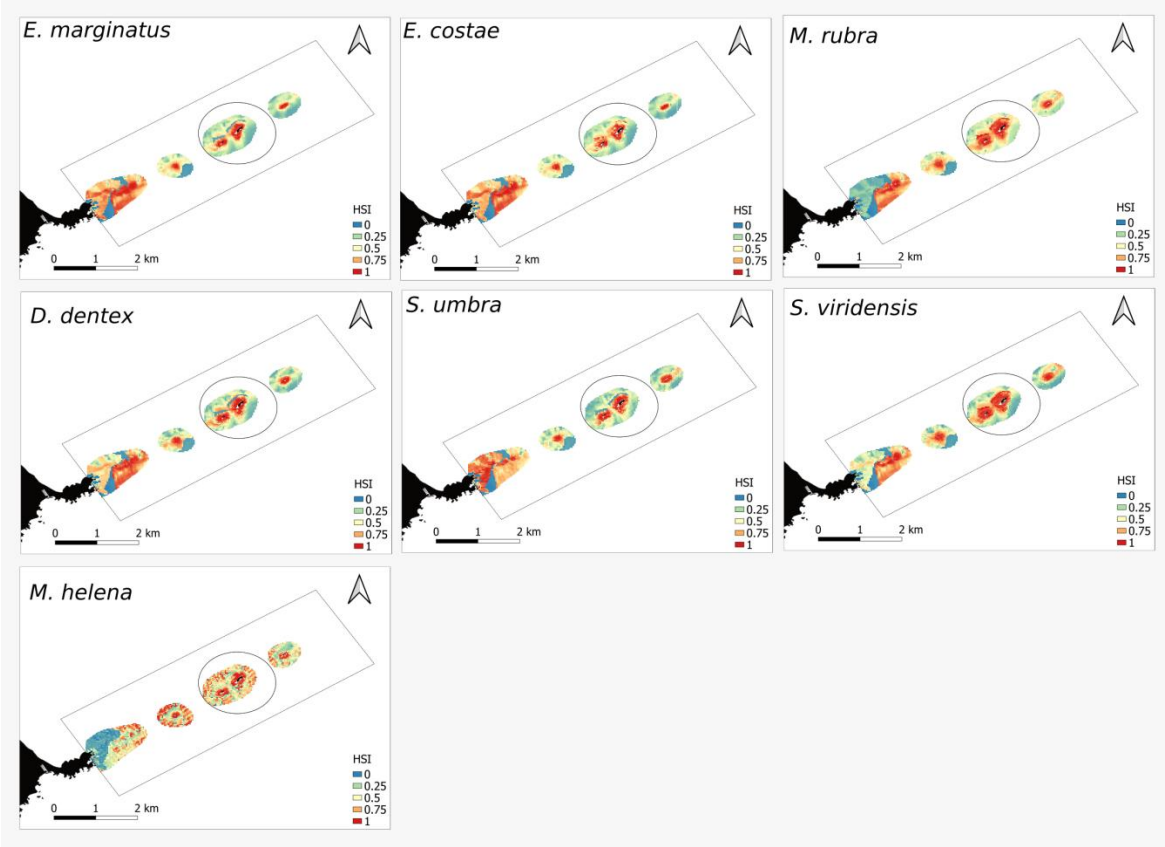


Figure 2. HSI maps (0 – 1) obtained for the species *E. marginatus*, *E. costae*, *M. rubra*, *S. umbra*, *D. dentex*, *S. viridensis* and *M. helena* in CP when considering all individuals together.

3.1.3. Mature individuals

All models showed a good fit (Boyce indices > 0.7). Marginality was high and similar for all species. However, it was greater than the marginality found for immature individuals. Marginality was determined by bathymetry, curvatures, rugosity, slope and TRI for all species, except for the species *S. viridensis* for rugosity and slope. Additionally, only *E. costae* and *S. viridensis* showed differences concerning immature individuals (Table 4). All species exhibited preferences for habitat 6 ("photophilic algae + red algae - urchins + pre-coral + caves - overhangs").

Specialization was high and similar for all species but lower than the one found for immature individuals, highlighting that mature individuals are less sensitive to changes in the environment. Most species showed a greater contribution of bathymetry, slope and TRI to specialization. Additionally, the specialization of *E. costae*

was also dependent on BPI and slope, and the one of *S. viridensis* on mean curvature and rugosity (Table 4).

In general, HS maps show a defined area of high HSI surrounding the seamounts and islands, however, not all species show the same patterns (Fig. 4).

Table 3. ENFA results, specifying A) Boyce index, B) the number of pixels with observations for each species, C) results of the total marginality and the contribution of the EGVs to marginality and D) total specialization and the contribution of the EGVs to specialization for each of the studied species in CP when considering immature individuals.

	E. costae	*D. dentex*	*E. marginatus*	*M. helena*	*M. rubra*	*S. umbra*	*S. viridensis*
A) Boyce index	0.52	0.69	0.95			0.62	0.92
Boyce I. 10%	0.50 ± 0.06	0.90 ± 0.07	0.93 ±0.03			0.78 ± 0.11	0.85 ± 0.07
B) Nº Pixels	12	32	50	-	4	19	18
C) Marginality	2.75	4.51	5.47			3.87	5.63
bathymetry	**1.26**	**1.29**	**1.24**	-	-	**1.44**	**1.38**
BPI	**1.21**	**1.65**	**2.62**	-	-	**1.36**	**2.67**
curvature	**1.03**	**1.49**	**2.54**	-	-	**1.22**	**2.50**
plan curv.	0.58	**1.18**	**1.83**	-	-	0.66	**1.93**
profile curv.	-0.99	**-1.37**	**-2.46**	-	-	**-1.28**	**-2.30**
eastness	-0.35	-0.92	-0.52	-	-	-0.64	**-1.00**
northness	-0.46	0.35	0.04	-	-	0.57	0.33
rugosity	0.72	**1.78**	**1.34**	-	-	**1.46**	**1.46**
slope	0.75	**1.77**	**1.32**	-	-	**1.52**	**1.46**
TRI	0.82	**1.78**	**1.37**	-	-	**1.52**	**1.44**
habitat 6	**1.08**	**8.96**	**7.56**	-	-	**8.39**	**8.24**
D) Specialization	5231.67	1478.58	612.83			14868.52	8326.59
bathymetry	**2.5E-02**	**1.7E-02**	**4.3E-02**	-	-	**2.8E-02**	7.0E-03
BPI	**4.9E-02**	2.1E-03	1.6E-03	-	-	2.3E-03	2.1E-03
curvatures	**3.6E-01**	3.6E-03	8.0E-04	-	-	7.1E-03	8.9E-03
plan curv.	**3.4E-02**	6.1E-05	5.3E-06	-	-	5.4E-03	2.7E-04
profile curv.	8.9E-02	7.3E-05	2.8E-05	-	-	7.8E-03	3.4E-04
eastness	2.0E-03	1.4E-04	1.9E-06	-	-	2.4E-03	2.0E-04
northness	6.2E-04	2.2E-06	1.9E-04	-	-	1.8E-05	1.4E-04
rugosity	6.7E-02	6.0E-05	**2.5E-02**	-	-	**1.7E-02**	**2.2E-02**
slope	4.9E-02	**1.3E-01**	**4.3E-02**	-	-	**1.1E-01**	**2.8E-01**
TRI	8.0E-03	**2.0E-01**	8.5E-03	-	-	**7.8E-02**	**5.1E-01**

BPI: bathymetry position index. TRI: terrain ruggedness index. Habitat 6: photophilic algae + red algae - urchins + pre-coral + caves – overhangs. Only significant habitat categories are shown in the table. The variables significantly contributing to marginality and specialization are highlighted in bold.

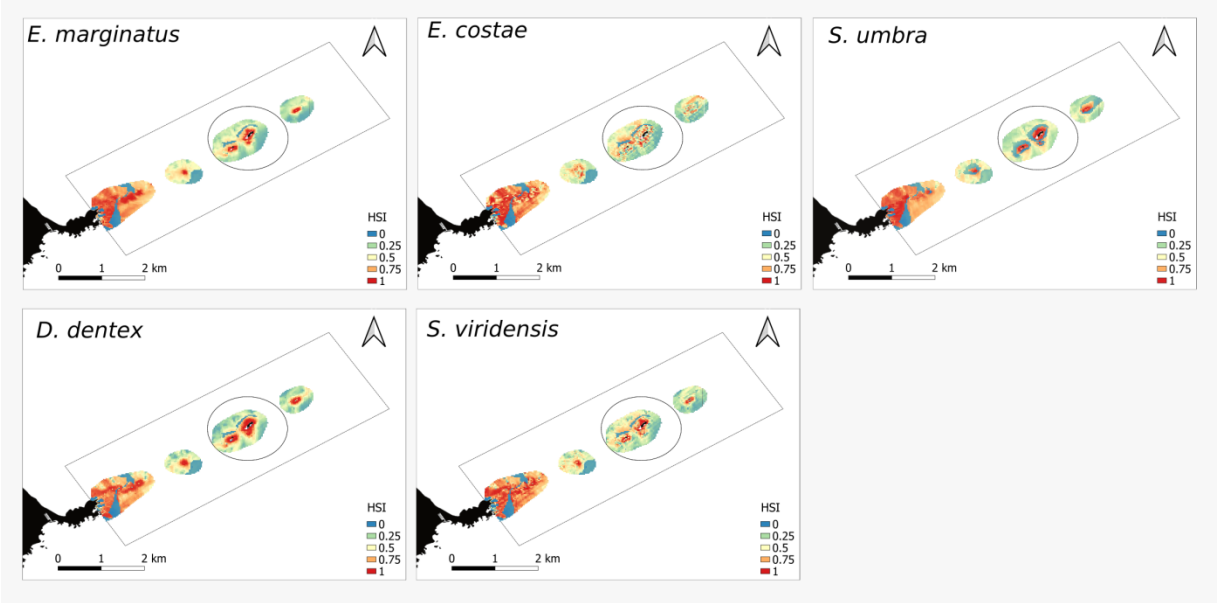


Figure 3. HSI maps (0 – 1) obtained for the species *E. marginatus*, *E. costae*, *M. rubra*, *S. umbra*, *D. dentex*, *S. viridensis* and *M. helena* in CP when considering immature individuals.

3.2. Cabo Tiñoso - Cabo Cope

3.2.1. ***All individuals***

Models with data issued from CTCC locations had a good fit for *E. costae*, *D. dentex*, *E. marginatus*, *M. helena* and *S. umbra* (Boyce indices > 0.7) and bad for *M. rubra* and *S. viridensis* (Boyce indices between 0.2 and 0.4). Marginality was similar among species and lower than the one found in CP, but with values still > 1, indicating that, even if values are not very large, habitats with observations are different from average habitats. All variables had a low contribution to marginality. The variables with a greater contribution were mostly bathymetry, variables describing habitat complexity and orientation (Table 5). All species showed preferences for habitat 6 ("photophilic algae + red algae - urchins + pre-coral + caves - overhangs"). Additionally, *D. dentex*, and *S. umbra* showed a predilection for habitat 24 ("*Posidonia oceanica* + *Cymodocea nodosa*), and 11 ("caves - overhangs + coral") in the case of *S. umbra*. *M. helena* showed also preferences for habitat 11, and *S. viridensis* exhibited priority for habitats 6 and 23 ("*Posidonia oceanica*").

Table 4. ENFA results, specifying A) Boyce index, B) the number of pixels with observations for each species, C) results of the total marginality and the contribution of the EGVs to marginality and D) total specialization and the contribution of the EGVs to specialization for each of the studied species in CP when considering mature individuals.

	E. costae	*D. dentex*	*E. marginatus*	*M. helena*	*M. rubra*	*S. umbra*	*S. viridensis*
A) Boyce index	0.87	0.89	0.86		0.75	0.82	0.97
Boyce I. 10%	0.80 ± 0.06	0.91 ± 0.06	0.89 ± 0.05		0.81 ± 0.12	0.87 ± 0.06	0.91 ± 0.04
B) Nº Pixels	44	53	56	-	41	24	31
C) Marginality	6.81	6.90	6.39		6.07	5.51	5.35
bathymetry	**1.20**	**1.19**	**1.19**	-	**1.34**	**1.44**	**1.27**
BPI	**3.36**	**3.29**	**3.10**	-	**2.83**	**2.52**	**2.64**
curvature	**3.27**	**3.24**	**3.03**	-	**2.69**	**2.40**	**2.55**
plan curv.	**3.01**	**2.75**	**2.45**	-	**2.73**	**1.60**	**2.21**
profile curv.	**-2.75**	**-2.94**	**-2.75**	-	**-1.91**	**-2.31**	**-2.17**
eastness	-0.60	-0.32	-0.51	-	-0.43	-0.71	-0.87
northness	-0.10	-0.12	-0.02	-	-0.16	0.14	0.16
rugosity	**1.38**	**1.68**	**1.49**	-	**1.67**	**1.62**	0.99
slope	**1.39**	**1.68**	**1.49**	-	**1.68**	**1.61**	1.00
TRI	**1.45**	**1.68**	**1.52**	-	**1.67**	**1.61**	**1.08**
habitat 6	**6.84**	**8.51**	**6.55**	-	**7.83**	**10.29**	**6.38**
D) Specialization	1142.59	688.49	760.13		1270.35	1986.35	1853.70
bathymetry	**3.5E-02**	**3.0E-02**	**3.8E-02**	-	**1.9E-02**	**1.9E-02**	**5.2E-02**
BPI	7.3E-04	1.7E-04	2.8E-04	-	1.9E-04	2.3E-04	**2.0E-02**
curvatures	5.2E-04	2.7E-05	2.9E-03	-	2.7E-03	1.3E-03	**4.8E-02**
plan curv.	5.5E-06	3.0E-05	1.1E-04	-	3.0E-04	2.9E-04	1.3E-03
profile curv.	2.0E-05	2.3E-04	4.9E-04	-	3.7E-04	1.2E-04	1.1E-03
eastness	8.5E-06	1.1E-04	1.9E-06	-	6.5E-05	1.6E-03	2.2E-05
northness	4.8E-05	1.5E-04	4.3E-05	-	1.3E-05	1.9E-06	5.3E-04
rugosity	**2.5E-03**	**1.5E-03**	**2.7E-02**	-	**9.5E-03**	**2.0E-02**	**1.4E-02**
slope	**1.7E-02**	**1.3E-01**	**4.9E-02**	-	**9.6E-02**	**1.4E-01**	**2.0E-02**
TRI	**2.4E-02**	**1.5E-01**	**1.5E-02**	-	**8.5E-02**	**9.4E-02**	2.1E-04

BPI: bathymetry position index. TRI: terrain ruggedness index. Habitat 6: photophilic algae + red algae - urchins + pre-coral + caves – overhangs. Only significant habitat categories are shown in the table. The variables significantly contributing to marginality and specialization are highlighted in bold.

Specialization was high for all species (> 76), being *S. viridensis* the species with the highest specialization (> 10 000). Moreover, *M. helena* had the lowest values (77). Specialization was mostly dependent on curvatures for all species, except *M. rubra*, for which it was dependent on orientation, rugosity and slope, and *S. viridensis*, for which it was dependent on bathymetry (Table 5).

Maps show that most coastal areas have greater values of HSI. However, slight differences were observed among species (Fig. 5).

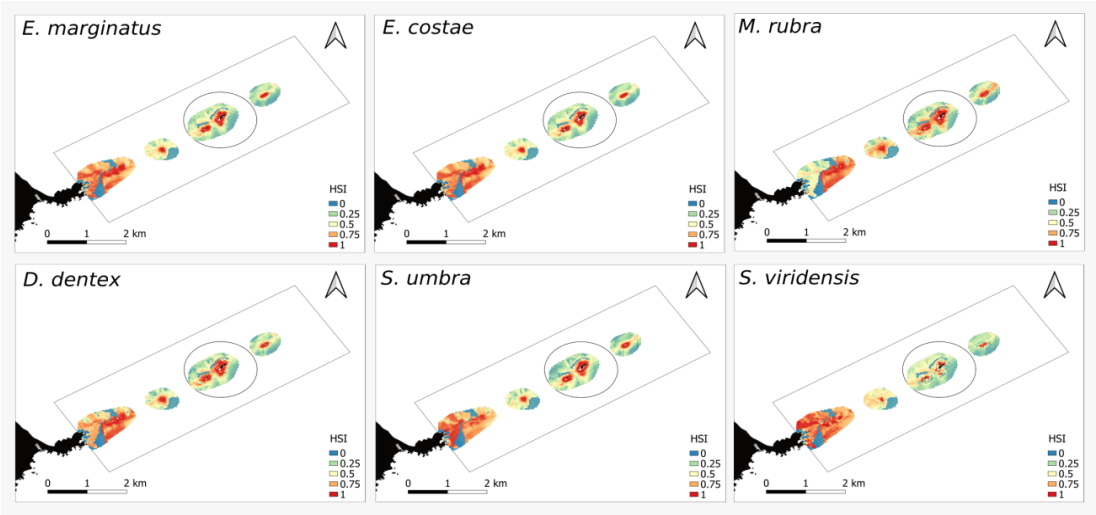


Figure 4. HSI maps (0 – 1) obtained for the species *E. marginatus*, *E. costae*, *M. rubra*, *S. umbra*, *D. dentex*, *S. viridensis* and *M. helena* in CP when considering mature individuals.

3.2.2. Immature individuals

Models showed a good fit for all species (Boyce indices > 0.7) except for *D. dentex* and *S. viridensis* (Boyce indices = 0). In addition to *M. helena*, the analysis was not possible to be performed with the species *M. rubra*, because of the low number of pixels with observations (Table 6).

Marginality was similar among species and the same order of magnitude as the marginality when individuals of all sizes were considered together. Marginality was determined by bathymetry for all species, and orientation for all species except *S. viridensis*. The other species showed different contributions of the variables to the marginality: *E. costae* was marginal for curvatures too, and *E. marginatus* for TRI. *S. viridensis* was the most different species, and the variables that contributed to marginality were northness, rugosity and TRI (Table 6).

Table 5. ENFA results, specifying A) Boyce index, B) the number of pixels with observations for each species, C) results of the total marginality and the contribution of the EGVs to marginality and D) total specialization and the contribution of the EGVs to specialization for each of the studied species in CTCC when considering all individuals together.

	E. costae	*D. dentex*	*E. marginatus*	*M. helena*	*M. rubra*	*S. umbra*	*S. viridensis*
A) Boyce index	0.73	1.00	0.85	0.81	0.52	0.80	0.54
Boyce I. 10%	0.75 ± 0.19	0.91 ± 0.07	0.92 ± 0.04	0.83 ± 0.09	0.26 ± 0.28	0.92 ± 0.05	0.48 ± 0.09
B) Nº Pixels	35	27	57	31	10	37	11
C) Marginality	1.23	1.54	1.25	1.48	2.01	1.54	1.68
bathymetry	**0.83**	**0.63**	**0.94**	**0.62**	**0.99**	**0.80**	**0.92**
BPI	-0.32	0.32	0.22	-0.24	**-0.77**	0.29	-0.21
curvature	-0.36	0.57	-0.02	-0.56	**-0.82**	0.38	-0.26
plan curv.	**-0.42**	0.44	-0.13	-0.62	**-0.90**	0.24	-0.47
profile curv.	0.29	**-0.63**	-0.07	0.48	0.69	-0.46	0.08
eastness	-0.24	**-0.64**	**-0.50**	-0.17	0.28	**-0.80**	-0.47
northness	0.03	-0.17	-0.19	0.08	0.03	-0.20	**0.72**
rugosity	0.31	0.38	0.30	**0.51**	0.42	0.43	**0.73**
slope	0.26	0.40	0.32	0.48	0.40	0.42	0.38
TRI	0.34	0.45	0.35	**0.53**	0.28	0.43	0.47
habitat 6	**5.41**	**6.07**	**5.45**	**5.99**	**5.87**	**3.80**	**4.25**
habitat 24	<1	**13.42**	<1	<1	<1	**1.14**	<1
habitat 11	<1	<1	<1	**2.16**	<1	**3.77**	<1
habitat 23	<1	<1	<1	<1	<1	<1	**2.76**
D) Specialization	136.77	150.80	162.84	76.99	374.57	455.15	10183.54
bathymetry	1.3E-04	4.0E-04	4.2E-05	1.6E-03	2.0E-03	1.6E-03	**3.9E-01**
BPI	7.7E-06	7.4E-07	5.4E-06	5.7E-05	5.0E-02	1.5E-04	2.0E-02
curvatures	**6.4E-01**	**6.4E-01**	**6.4E-01**	**6.3E-01**	2.2E-03	**6.4E-01**	7.0E-03
plan curv.	**1.4E-01**	**1.4E-01**	**1.4E-01**	**1.4E-01**	4.2E-03	**1.3E-01**	5.5E-04
profile curv.	**2.1E-01**	**2.1E-01**	**2.2E-01**	**2.1E-01**	3.5E-03	**2.2E-01**	1.9E-02
eastness	4.3E-06	1.0E-05	1.4E-05	7.5E-05	**2.9E-01**	5.1E-07	1.3E-03
northness	6.1E-05	3.1E-04	4.0E-05	5.1E-04	**3.1E-01**	1.8E-04	7.9E-03
rugosity	8.1E-04	2.4E-03	3.4E-04	4.2E-03	**1.2E-01**	1.5E-03	6.1E-03
slope	4.2E-04	8.1E-04	2.9E-04	2.9E-03	**2.0E-01**	2.1E-04	2.3E-02
TRI	4.1E-04	5.7E-04	2.6E-05	4.2E-04	6.9E-03	6.9E-04	8.6E-03

BPI: bathymetry position index. TRI: terrain ruggedness index. Habitat 6: photophilic algae + red algae - urchins + pre-coral + caves - overhangs. Habitat 24: *Posidonia oceanica* + *Cymodocea nodosa*. Habitat 11: caves - overhangs + coral. Habitat 23: *Posidonia oceanica*. Only significant habitat categories are shown in the table. The variables significantly contributing to marginality and specialization are highlighted in bold.

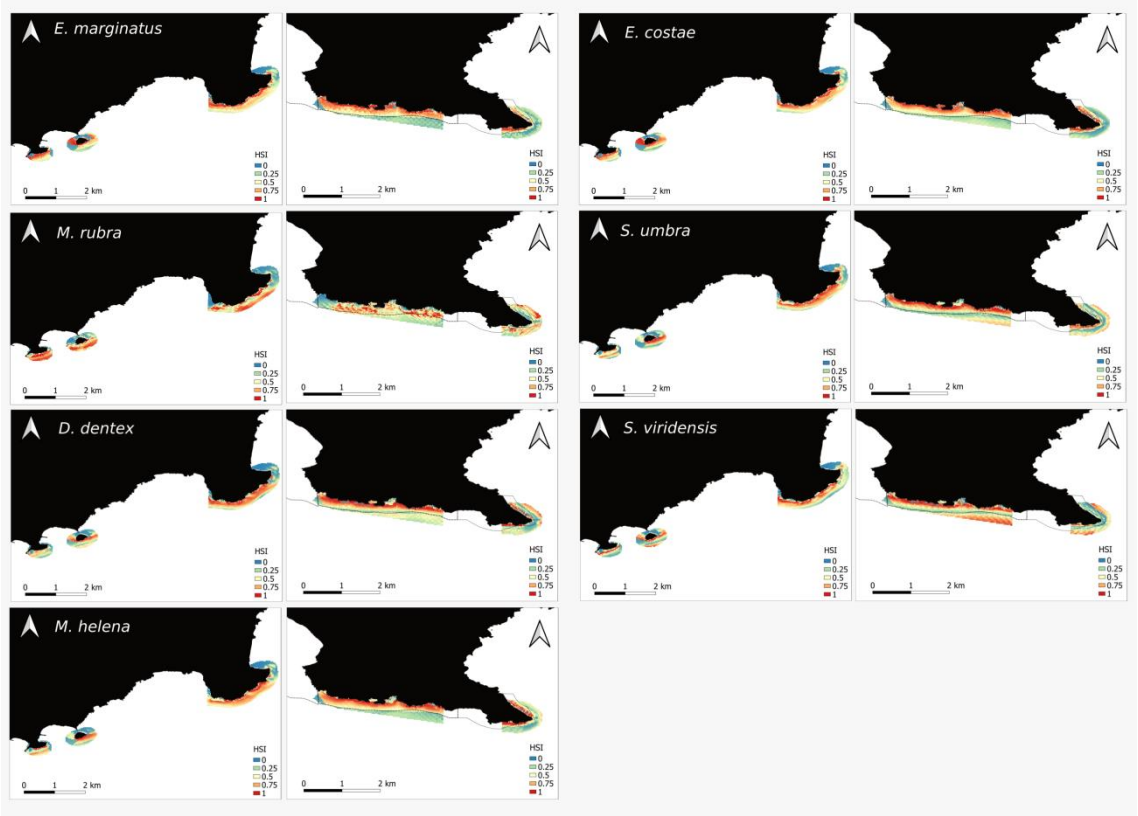


Figure 5. HSI maps (0 – 1) obtained for the species *E. marginatus*, *E. costae*, *M. rubra*, *S. umbra*, *D. dentex*, *S. viridensis* and *M. helena* in CTCC when considering all individuals together.

All species showed preferences by habitat 6 ("photophilic algae + red algae - urchins + pre-coral + caves - overhangs"). Additionally, *D. dentex* showed a predilection for habitat 24 ("*Posidonia oceanica* + *Cymodocea nodosa*), *S. umbra* for habitat 11 ("caves – overhangs + coral"), and *S. viridensis* for habitat 23 ("*Posidonia oceanica*").

Specialization was high (> 58) and similar among species. Though, it was lower than the one found for all individuals of all species taken together. Specialization was mostly determined by curvatures for *E. costae*, *E. marginatus* and *S. umbra*. Moreover, *D. dentex* showed a greater contribution of BPI and plan curvature, and *S. viridensis* showed a greater importance of BPI and slope to specialization (Table 6).

HS maps show a narrow area next to the coast with high values of HS for *S. umbra*, *E. marginatus* and *D. dentex* in CT, though, in CC the area is larger and the area greater (Fig. 6). *E. costae* and *S. viridensis* show different patterns. *E. costae* shows a

narrow area but further from the coastline, and *S. viridensis* shows a patchy distribution of high HS (Fig. 6).

Table 6. ENFA results, specifying A) Boyce index, B) the number of pixels with observations for each species, C) results of the total marginality and the contribution of the EGVs to marginality and D) total specialization and the contribution of the EGVs to specialization for each of the studied species in CTCC when considering immature individuals.

	E. costae	*D. dentex*	*E. marginatus*	*M. helena*	*M. rubra*	*S. umbra*	*S. viridensis*
A) Boyce index	0.84	0.52	0.84			0.90	0.00
Boyce I. 10%	0.88 ± 0.07	0.05 ± 0.16	0.86 ± 0.07			0.89 ± 0.06	0
B) Nº Pixels	25	10	53	-	4	32	10
C) Marginality	1.26	1.06	1.23			1.64	1.68
bathymetry	**0.93**	**0.69**	**0.99**	-	-	**0.77**	**0.90**
BPI	-0.27	-0.23	0.17	-	-	0.38	-0.07
curvature	**-0.33**	0.09	-0.08	-	-	0.46	-0.16
plan curv.	**-0.34**	-0.05	-0.18	-	-	0.31	-0.34
profile curv.	**0.31**	-0.20	-0.01	-	-	-0.54	0.00
eastness	**-0.35**	**-0.61**	**-0.47**	-	-	**-0.80**	-0.32
northness	-0.13	-0.25	-0.11	-	-	-0.19	**0.65**
rugosity	0.22	0.15	0.28	-	-	0.48	**0.83**
slope	0.22	0.19	0.27	-	-	0.47	0.51
TRI	0.29	0.22	**0.31**	-	-	0.48	**0.62**
habitat 6	**5.68**	**3.58**	**5.32**	-	-	**3.98**	**3.31**
habitat 24	<1	**39.86**	<1	-	-	<1	<1
habitat 11	<1	<1	<1	-	-	**3.92**	<1
habitat 23	<1	<1	<1	-	-	<1	**2.09**
D) Specialization	387.73	58.50	126.62			593.26	1757.95
bathymetry	6.2E-05	1.9E-02	6.9E-05	-	-	4.9E-04	2.9E-02
BPI	1.7E-05	**2.7E-01**	4.7E-05	-	-	1.6E-04	**4.8E-01**
curvatures	**6.4E-01**	3.3E-02	**6.4E-01**	-	-	**6.4E-01**	2.8E-02
plan curv.	**1.4E-01**	**3.6E-01**	**1.3E-01**	-	-	**1.3E-01**	5.2E-03
profile curv.	**2.2E-01**	3.6E-02	**2.2E-01**	-	-	**2.2E-01**	5.1E-02
eastness	1.8E-05	7.5E-02	2.9E-05	-	-	1.2E-06	5.6E-02
northness	1.9E-05	1.7E-02	8.7E-05	-	-	1.2E-04	6.5E-02
rugosity	2.4E-04	3.3E-02	5.8E-04	-	-	1.3E-03	4.3E-02
slope	1.6E-04	5.1E-02	6.2E-04	-	-	6.6E-04	**2.3E-01**
TRI	3.8E-04	2.9E-02	1.2E-04	-	-	2.7E-04	6.9E-03

BPI: bathymetry position index. TRI: terrain ruggedness index. Habitat 6: photophilic algae + red algae - urchins + pre-coral + caves - overhangs. Habitat 24: *Posidonia oceanica* + *Cymodocea nodosa*. Habitat 11: caves - overhangs + coral. Habitat 23: *Posidonia oceanica*. Only significant habitat categories are shown in the table. The variables significantly contributing to marginality and specialization are highlighted in bold.

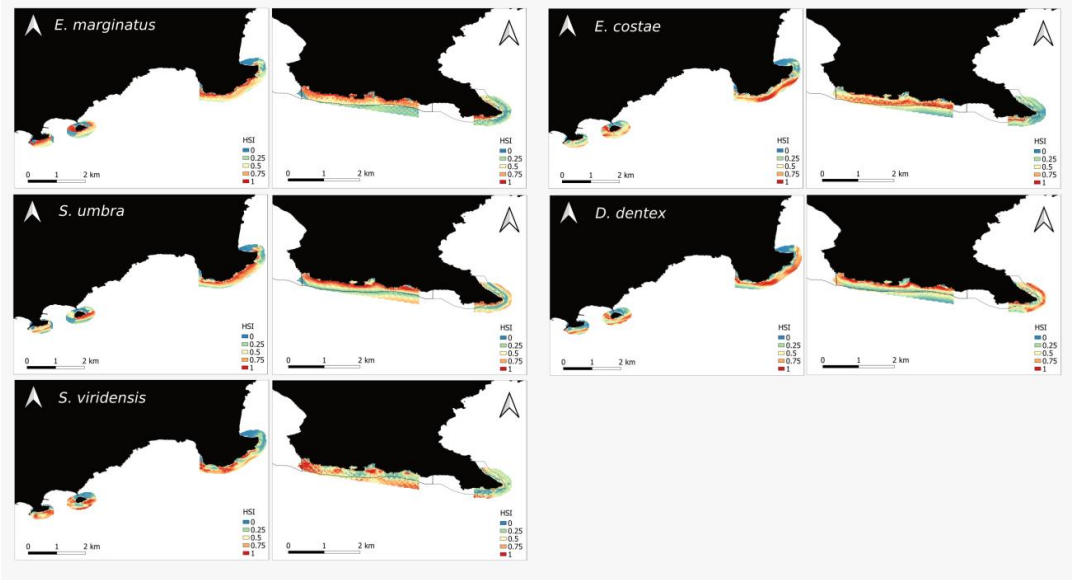


Figure 6. HSI maps (0 – 1) obtained for the species *E. marginatus*, *E. costae*, *M. rubra*, *S. umbra*, *D. dentex*, *S. viridensis* and *M. helena* in CTCC when considering immature individuals.

3.2.3. Mature individuals

Models fit was good for *D. dentex* (Boyce index > 0.8), moderate for *E. costae* (Boyce index = 0.47) and deficient for *E. marginatus* and *S. umbra* (Boyce index < 0.3). The analyses were not possible to be performed, in addition to *M. helena*, with the species *M. rubra* and *S. viridensis*, because the number of pixels with observations was too low (< 5) (Table 7).

Marginality was low and similar to the marginality found for immature individuals. It was mainly determined by bathymetry. However, the contribution of the other variables to marginality was variable among species. *E. costae* was marginal for plan curvature, rugosity and TRI. *D. dentex* for mean and profile curvatures, and eastness. *E. marginatus* for eastness, slope and TRI. And *S. viridensis* for eastness, BPI, and mean and profile curvatures (Table 7). All species showed preferences for habitat 6 ("photophilic algae + red algae - urchins + pre-coral + caves - overhangs"). Additionally, *D. dentex* showed a predilection for habitat 24 ("*Posidonia oceanica* + coastal detrital).

Specialization was high for all species and greater than the values found for immature individuals, except for *E. costae*, in which the patterns were the opposite.

Specialization was determined by curvatures for *E. costae* and *D. dentex*, rugosity and slope for *E. marginatus*, and plan curvature for *S. viridensis* (Table 7).

HS maps show that the mature of *S. umbra* and *E. costae* appear nearer to the coastline than immature individuals in CC but further in CT. Mature individuals of *E. marginatus* and *D. dentex* appear further to the coastline both in CT and CC (Fig. 7).

Table 7. ENFA results, specifying A) Boyce index, B) the number of pixels with observations for each species, C) results of the total marginality and the contribution of the EGVs to marginality and D) total specialization and the contribution of the EGVs to specialization for each of the studied species in CTCC when considering mature individuals.

	E. costae	*D. dentex*	*E. marginatus*	*M. helena*	*M. rubra*	*S. umbra*	*S. viridensis*
A) Boyce index	0.64	0.92	0.38			0.52	
Boyce I. 10%	0.48 ± 0.14	0.81 ± 0.10	0.30 ± 0.22			0.16 ± 0.25	
B) Nº Pixels	15	24	11	-	5	10	4
C) Marginality	1.45	1.71	1.41			1.90	
bathymetry	**0.65**	**0.63**	**1.05**	-	-	**0.71**	-
BPI	-0.42	0.51	-0.18	-	-	**0.67**	-
curvature	-0.46	**0.66**	-0.16	-	-	**0.63**	-
plan curv.	**-0.61**	0.57	-0.15	-	-	0.52	-
profile curv.	0.32	**-0.68**	0.16	-	-	**-0.66**	-
eastness	0.07	**-0.65**	**0.42**	-	-	**-0.74**	-
northness	0.18	-0.14	0.35	-	-	-0.14	-
rugosity	**0.51**	0.42	-0.27	-	-	0.58	-
slope	0.43	0.44	**-0.44**	-	-	0.57	-
TRI	**0.56**	0.47	**-0.47**	-	-	0.56	-
habitat 6	**5.83**	**6.38**	**6.84**	-	-	**4.21**	-
habitat 24	<1	**11.85**	<1	-	-	<1	-
habitat 11	<1	<1	<1	-	-	<1	-
habitat 23	<1	<1	<1	-	-	<1	-
D) Specialization	232.46	185.45	5557.71			820.23	
bathymetry	4.5E-04	3.9E-03	7.8E-03	-	-	8.6E-02	-
BPI	4.6E-05	1.7E-05	3.6E-02	-	-	4.2E-02	-
curvatures	**6.4E-01**	**6.3E-01**	5.6E-02	-	-	3.8E-04	-
plan curv.	**1.4E-01**	**1.4E-01**	8.4E-03	-	-	**1.5E-01**	-
profile curv.	**2.1E-01**	**2.1E-01**	1.4E-03	-	-	7.6E-02	-
eastness	3.5E-05	1.2E-04	6.5E-05	-	-	1.3E-02	-
northness	1.7E-04	1.3E-03	3.0E-02	-	-	1.6E-02	-
rugosity	3.3E-03	6.6E-03	**4.3E-01**	-	-	6.4E-02	-
slope	6.2E-03	7.0E-04	**4.2E-01**	-	-	6.1E-02	-
TRI	1.5E-03	4.1E-03	7.3E-03	-	-	3.6E-03	-

BPI: bathymetry position index. TRI: terrain ruggedness index. Habitat 6: photophilic algae + red algae - urchins + pre-coral + caves - overhangs. Habitat 24: *Posidonia oceanica* + *Cymodocea nodosa*. Habitat 11: caves - overhangs + coral. Habitat 23: *Posidonia oceanica*. Only significant habitat categories are shown in the table. The variables significantly contributing to marginality and specialization are highlighted in bold.

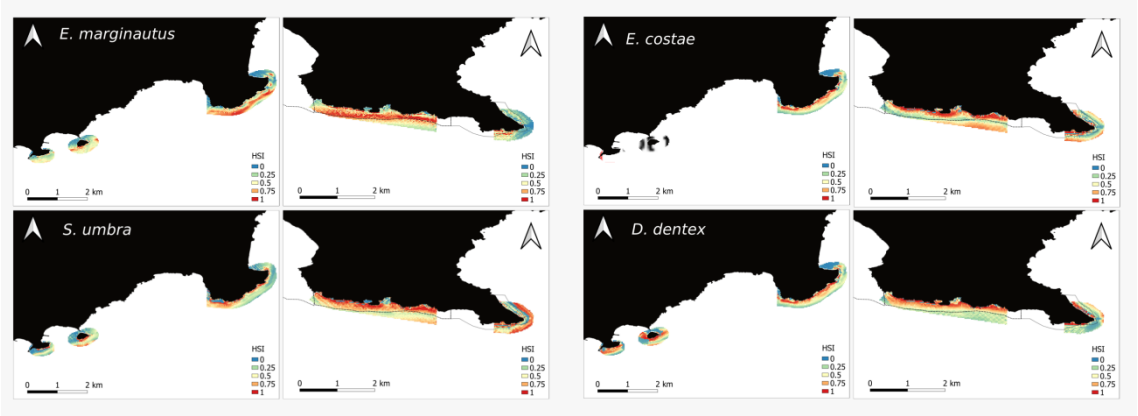


Figure 7. HSI maps (0 – 1) obtained for the species *E. marginatus*, *E. costae*, *M. rubra*, *S. umbra*, *D. dentex*, *S. viridensis* and *M. helena* in CTCC when considering mature individuals.

4. Discussion

Understanding the environmental variables that explain the occurrence of ecological and economic important species and the spatial location of their suitable habitats is essential for the correct establishment of MPAs (Abecasis *et al.* 2014, Sánchez-Carnero *et al.* 2016). Moreover, the identification of the suitable habitat for different life stages allows for predicting the ecological benefits of the studied areas (Gailaduk *et al.* 2018). In this study, by means of ENFA SDMs, we assessed the environmental factors, characterized by sea bottom features and benthic habitat types, which better describe the occurrence of high-level predatory species in the Region of Murcia (SE Spain), in protected and unprotected areas with different density of fish, and according to the maturity stages of the species.

Model selection and fitting

Presence-only models are especially useful tools for modelling habitat suitability of marine fish because they do not need the inclusion of absence data. In the case of mobile marine fish, the fact that sightings have been gathered in an area does not necessary means that fish are absent in other areas (Monk *et al.* 2010). Additionally, marine surveys have usually low observation data, and most presence-only models perform well with few observations (Engler *et al.* 2004, Hernández *et al.* 2006). Indeed, despite our analyses have limited observation data, model performance was generally

good (Boyce index = 0.73 ± 0.13, mean ± SE). In our case, Boyce indices performed better (> 0.7) when the number of observations was greater than 15 pixels. This has been previously discussed in Sánchez-Carnero *et al.* (2016), in which models with less than 10 samples for calculations gave a worse model performance with large deviations.

There is a wide array of presence-only models, such as DOMAIN (Carpenter *et al.* 1993), BIOCLIM (Hijmans & Graham 2006), Maximum Entropy (MaxEnt; Philips *et al.* 2006) or ENFA. All these algorithms provide a habitat suitability map, which reflects the distribution of the species based on environmental characteristics. However, the statistical assumptions vary among models. In this study, we have chosen ENFA because it is simpler, both algorithmically and in terms of its ecological interpretation (Sánchez-Carnero *et al.* 2016). Moreover, ENFA provides values of marginality and specialization for each species and the contribution of the environmental variables to those measurements (Hirzel *et al.* 2001, 2002). This additional information allows us to understand the different selection of the species in the whole area of study, increasing knowledge on the requirements of these species. Another advantage of using ENFA is the possibility to identify the most parsimonious interpretation of the results in terms of input information, which can be achieved through the weights of EGVs in the marginality and specialization in ENFA (Sánchez-Carnero *et al.* 2016), as was done in the present study.

Other issues that vary among SDM approaches are the multidimensionality and the sampling bias. A big number of variables is a key concern for models such as MaxEnt, which generates new features from input variables, increasing drastically the number of variables as well as the processing time; in this particular case, performing a PCA or similar analysis is recommended to reduce multidimensionality (Merow *et al.* 2013). For its part, ENFA method uses only the input variables, so computing times are lower. Moreover, since it performs an orthogonal transformation of the variables, the correlation among them is not a problematic issue (Hirzel *et al.* 2002). Sampling bias is present in most occurrence data, representing a problem for SDM in general: when sampling is biased, it is not possible to discriminate those cases in which the species is observed in particular areas because they prefer them from those cases in which the

sampling effort was bigger in these areas (Chakraborty *et al.* 2011). To reduce this problem, in this work we have diminished the study area to an area where sampling effort could be considered similar.

Although several recent contributions still rely on a single model approach (Galaiduk *et al.* 2018, Davis 2019, Sinopoli *et al.* 2019, Zellmer *et al.* 2019), recently many authors are suggesting the use of several models in order to undergo the uncertainties associated with model selection and improve the predictions (Caradima *et al.* 2019, França *et al.* 2019, Norberg *et al.* 2019, Tobler *et al*. 2019, Thuiller *et al.* 2019), which would suppose a further refinement of this methodology after the present first approach to modelling habitat suitability of the species of interest.

Habitat selection at different fish densities

Our results show similarities in the variables contributing to species distribution in the CP and CTCC areas, although there are some variations. In CP, all species showed a greater contribution of bathymetry and variables describing habitat complexity (i.e. BPI, rugosity, slope, TRI) to marginality and specialization; moreover, all species preferred rocky habitats with algae and caves. Therefore, in this marine reserve the studied fish species were preferably observed in complex and heterogeneous (*sensu* García-Charton & Pérez-Ruzafa 2001) rocky habitats at restricted depth fringes, which coincides with other habitat studies in the Mediterranean previously performed for the same species (e.g. García-Charton *et al.* 2004, Reñones *et al.* 2012). In our study, species appeared at depths lower than 40 m, indicating that even with potential habitats available in deeper areas, they are not selected by the studied species. At lower depths, the availability of light is greater, so is also the primary productivity (Sigman & Hain 2012). There are many studies performed with marine fish in which bathymetry appears as an important variable modulating species distribution (e.g. Monk *et al.* 2010, 2011, Saul *et al.* 2013, Abecasis *et al.* 2014, Gómez *et al.* 2015, Wedding & Yoklavich 2015, Zellmer *et al.* 2019). Moreover, habitats with high complexity have been identified to be more profitable for many fish species (García-Charton & Pérez-Ruzafa 2001, García-Charton *et al.* 2004, Pittman *et al.* 2011, Abecasis *et al.* 2014), as they provide refuge and shelter against predators and increase

accessibility to food (Gratwicke & Speight 2005, Claudet *et al.* 2011). Values of specialization were similar among species except for *M. helena,* which was higher than the other studied species. This may be due to the behavior of the species, as *M. helena* appears mostly hidden inside cracks and holes during the day, and comes out at night to feed (Louisy 2002); thus, its more restricted range of variables might be due to the more specialized behavior of the species.

In CTCC, marginality was similar among species and lower than in CP, which means that contrarily to the pattern found in the latter location, habitat occupied by them is more similar to the average habitat in the area. However, habitat structure in CTCC is more homogeneous along the rocky area than in CP, which may explain the lower marginality found. The variables that contributed the most to marginality were bathymetry, several variables describing habitat complexity (i.e. BPI, curvatures, rugosity, slope and TRI) and, contrary to CP, eastness, although there were slight differences among species. The fact that eastness (i.e. orientation towards the east) appears with a high contribution to marginality may be related to enhanced primary production in the most eastern area, favoured by the predominant winds, which could increase local upwellings. Predominant winds run from east and north-east, which in turn are responsible of ocean circulation and mixing of the upper layers, thus probably driving an increase in nutrients in the euphotic zone and augmenting locally the primary productivity (Chavez *et al.* 2010). Additionally, all species preferred rocky habitats with algae and caves, although other habitats, such as caves – overhangs with coral, *P. oceanica* or mixed meadows of *P. oceanica* and *C. nodosa* were important for some of the species. These types of habitat have been previously found to be important for the species (García-Charton *et al.* 2004, Harmelin-Vivien *et al.* 2015). Thus, it may be possible that the inclusion of several habitats increases habitat heterogeneity, which benefits the species. For all individuals, specialization was high and similar among species, except for *S. viridensis*, for which specialization was the highest. This may be because the species is pelagic, in contrast to the other species. Moreover, *S. viridensis* may be seen isolated or in couples, but is frequently found in shoals of up to hundreds of individuals (Barreiros *et al.* 2002), what may explain the differences found. All species showed a greater contribution of curvatures to

specialization. Curvatures are associated with exposure to currents and the nature of the seabed (Wilson *et al.* 2007). Areas with higher curvatures may have greater habitat complexity and increased water currents, and thus enhance primary productivity (Chavez *et al.* 2010).

All species appeared with greater specialization in the area of CP than in CTCC. Both marginality and specialization are variables related to the area of study. Because the ranges of the EGVs are not similar in the two areas (Table 1), absolute values are not comparable. However, it is possible to interpret the differences in the patterns found. Density-dependent habitat selection has been widely identified in nature and relies on the assumption that increasing densities would lead to species moving to marginal habitats with less productivity due to competition for the resources and predation (e.g. Lindberg *et al.* 2006, Paterson & Blouin-Demers 2018). However, two main aspects may be preventing from identifying these patterns in CP, despite the very high densities reached in this location. Firstly, in CP habitat is not continuous in all the MPA, as there are sedimentary bottoms between the seamounts and islands, while in CTCC habitat is continuous in all area. This may prevent fish from finding new marginal habitats in CP, but allow species to have wider movement ranges in CTCC. Moreover, food supply in CP is particularly high, and much greater than in CTCC, as the steep topography of seamounts and islands likely enhance local primary productivity by creating strong currents and swirls that would boost phytoplankton biomass and associated increment in zooplankton biomass, which in turn would favour the concentration of huge shoals of small pelagic species (e.g. *Boops boops*); in addition, the rocky outcrops could act as a visual reference for these species. This situation may contribute to the greater densities and very concentrated habitats found in CP when compared to CTCC, as a realization of the pelagic energetic-subsidy hypothesis (Beaudreau and Essington 2011, Trebilco *et al.* 2016).

Habitat selection at different maturity stages

In CP, marginality was greater for mature than immature individuals, with bathymetry and habitat complexity (i.e. BPI, curvatures, rugosity, slope and TRI) generally contributing the most to this model parameter. The different marginalities among

immatures and matures may be explained because immature individuals appeared more frequently in the most coastal area, where rocky reefs are shallower, and habitat is less complex - since habitat complexity increases with depth in the area; thus bottom features are more similar to the mean features of the entire area, which includes sedimentary bottoms in addition to the rocky seamounts and islands. Previous studies have found evidence that juvenile reef fish appear at shallower areas, and fish tend to move to deeper areas as they become older (La Mesa *et al.* 2006, Hackradt 2012, Reñones *et al.* 2012, Álvarez-Berastegui *et al.* 2018). Our study did not include juveniles but only immature adults. However, the results for immatures suggest that habitat selection is different than mature adults, and could be intermediate among juveniles and matures. Indeed, Álvarez-Berastegui *et al.* (2018) found that depth showed a negative effect on the density of juveniles while depth and roughness had a positive effect on the density of adults; importantly, these authors differentiated juveniles and adults of *E. marginatus* using length at maturity (i.e. juveniles < 50 cm, adults > 50 cm), therefore using the same size classification as us. Moreover, a study performed in Mexico with *Epinephelus morio* found that pre-adults were located in transition substrates between juveniles and adults (Albañez-Lucero & Arreguín-Sánchez, 2009), which support our findings. On the other hand, in CP specialization was greater for immature than mature individuals, indicating that in earlier life stages fish are more susceptible to changes in habitats than older fish, because the range of the variables was more restricted for immature than mature individuals. In freshwater fish, it has been found that pre-adult fish are more sensitive to habitat changes and represents a crucial stage in the life cycles (Van der Lee & Koops 2016). Larger and older fish gain survival advantage over smaller fish, which has traditionally known as the "bigger is better" hypothesis. Following this hypothesis, larger conspecific individuals would increase resistance to starvation, the ability to avoid predators, and resistance to environmental changes (Sogard 1997), which may explain the differences found.

In CTCC, marginality was lower than in CP, and similar among immature, mature and all individuals, which may be explained as the more homogeneous structure in the area, as previously pointed out. There was not a clear pattern in

specialization among immature and mature individuals in this area, as values were similar for *E. costae* and *S. umbra*, while *D. dentex* and *E. marginatus* showed greater specialization in mature individuals. All species showed a greater contribution of curvatures to specialization. Curvatures are associated with exposure to currents and the nature of seabed (Wilson *et al.* 2007). Areas with higher curvatures may have greater habitat complexity, and increased water currents and thus enhance primary productivity (Chavez *et al.* 2010).

HS maps and MPA suitability

In CP, there was a tendency of immatures to be restricted to the coastal area and the shallowest seamounts and islands, while matures were found at deeper zones and occupied wider areas. Thus, the CP MPA included high suitable habitats for both immature and mature individuals of all studied species, indicating that the MPA is effective at protecting the habitat requirements for different life stages of the studied species.

In turn, HS maps do not show clear patterns in CTCC among immature and mature individuals. For any species, though, results show areas of high suitability included in the studied locations. Particularly, the no-take zone of CT appears suitable for all species in any moment of their life-cycle, thus the spatial zoning in the MPA seems beneficial for the studied species. Moreover, in CC there are also areas of high suitability, which provides important information regarding the future establishment of an MPA in this area.

In conclusion, the present study demonstrates that valuable information regarding the habitat preference of emblematic species can be obtained using relatively simple methods – in our case, geo-referenced fish-presence data derived from low-cost visual methods, i.e. TRT+DS and/or towed video-camera, and habitat and bathymetric mapping issued from ship-borne acoustic surveys. This information can be readily used when designing new MPAs. Specifically, we found that the studied species (high-trophic level fishes) change their habitat requirements throughout their life cycles. Variables accounting for variations in depth and habitat complexity generally appeared as modulators of the distribution of the species in the studied

locations, highlighting the necessity of understanding the essential habitats for target species, and the importance of identifying these types of habitats when designing the implementation of an MPA. Both MPAs included in this study present zones with high habitat suitability for the studied species, supporting the need to be included in MPAs to ensure their effectiveness. Additionally, the unprotected area of CC includes high suitable habitats as well, which should be taken into account when designing the new MPA which is planned in the area, contributing by this mean to the establishment of an effective regional MPA network.

5. Appendices

Appendix A. Habitat types present in each of the study areas CP (Cabo de Palos-Islas Hormigas marine reserve) and CTCC (Cabo Tiñoso marine reserve and the unprotected Cabo Cope)

Cabo de Palos- Islas Hormigas MPA	
6	Photophilic algae + red algae - urchins + pre-coral + caves - overhangs
7	Infralittoral photophilic algae + *Posidonia oceanica*
11	Caves - overhangs + coral
12	Caves - overhangs + coral + coastal detrital
13	Coral + *Posidonia oceanica*
17	Fine sand
23	*Posidonia oceanica*
28	Coastal detrital
Cabo Tiñoso MPA - Cabo Cope	
1	Supra/midlittoral rocks
4	Supra/midlittoral rocks+photophilic algae+molluscs
5	Sciaphilic and photophilic algae+red algae-urchins
6	Photophilic algae + red algae - urchins + pre-coral + caves - overhangs
7	Infralittoral photophilic algae + Posidonia oceanica
11	Caves - overhangs + coral
16	Supra- and midlittoral peebles
17	Fine sand
19	Detrital mud
22	Sand + *Cymodocea nodosa* + *Zostera noltii*
23	*Posidonia oceanica*
24	*Posidonia oceanica*+coastal detrital
27	*Posidonia oceanica*+*Zostera nolttii*+*Cymodocea nodosa*
34	*Cymodocea nodosa*
39	Fine sand+Detrital mud

GENERAL

DISCUSSION

Contribution of the thesis to predatory fish ecology and MPA effectiveness

Understanding the ecological processes underlying the recovery of predatory fish in Marine Protected Areas is of great interest for several reasons. On the one hand, this information allows for increasing knowledge in this valuable group, in which many populations are under threat (IUCN 2017). Moreover, assessing the ecological processes that allow the recovery of predatory fish populations in MPAs enables the identification of the most ecologically effective MPA features (e.g. Micheli *et al.* 2004, Guidetti *et al.* 2008). As a result, MPA management may be enhanced by increasing efforts in some aspects of the administration of the natural resources, and new MPA establishment can be better designed to fulfill conservation objectives. This thesis evaluates some of the ecological processes underlying the conservation of predatory fish in MPAs, such as the effects of the regulation of fishing pressure, the effects of long-term protection and a temporal lack of surveillance in the recovery patterns, and the effects of the environmental features in the probability of occurrence of the species. Thus, the information gathered will help to both increase knowledge in the ecology of the selected predatory species and provide guidance on MPA management.

In the last decades, many efforts have been made to identify the most effective MPA features to increase their ecological effectiveness (Côté *et al.* 2001, Halpern & Warner 2002, Halpern 2003, Micheli *et al.* 2004, Claudet *et al.* 2008, Guidetti & Sala 2007, Guidetti *et al.* 2008, Di Franco *et al.* 2009, Claudet *et al.* 2010, Edgar *et al.* 2014, Giakoumi *et al.* 2017). Our results show that small but well enforced MPAs appear as effective tools for the conservation of predatory fish worldwide (Chapter I). The importance of enforcement to achieve an effective protection has been widely accepted (Guidetti *et al.* 2008, Edgar *et al.* 2014, Giakoumi *et al.* 2017). However, traditionally many experts have suggested the implementation of large no-take zones to increase MPA effectiveness (Halpern 2003, Claudet *et al.* 2008, Friedlander *et al.* 2017, Davies *et al.* 2017). Indeed, there are a number of advantages of implementing large MPAs. First, large-sized MPAs constitute a solution for achieving global protection targets on time, such as the Aichi Biodiversity Target 11 (Wilheim *et al.*

2014). Additionally, large MPAs usually encompass several ecosystems and habitats, allow for the connectivity among ecosystems, and promote greater ecological resilience against global change (Wilheim *et al.* 2014, Davies *et al.* 2018, O'Leary *et al.* 2018). However, there are a number of challenges related to the implementation of big MPAs. On the one hand, they are usually a result of political processes more than scientific tools (O'Leary *et al.* 2018), and are mostly located in remote areas, in which human pressure is low, thus ecological effectiveness may be reduced (Singleton & Roberts 2014, O'Leary *et al.* 2018); actually, we should beware of using these large MPAs as a shortcut to meet international objectives too quickly, without fulfilling all the requirements for an effective protection of marine ecosystems (Giglio *et al*. 2018). Additionally, large MPAs imply several social conflicts (Singleton & Roberts 2014, Davies *et al.* 2018) when designated in areas next to local populations, and the investment to allow an effective surveillance may be too large to achieve the expected results (Wilhelm *et al.* 2014). Hence, in areas in which livelihoods are strongly related to the sea, the implementation of several small and well enforced MPAs may act as a solution both economically and for social aspects (Giakoumi *et al.* 2017).

Although previous studies have found that buffer zones are less effective than no-take zones (Lester *et al.* 2009, Claudet *et al.* 2008, Sciberras *et al.* 2013, Giakoumi *et al.* 2017, Sala & Giakoumi 2017), they can be useful tools for conservation if properly designed and managed and are an intermediate solution for the protection of the resources while keeping some anthropogenic activities (Hackradt *et al.* 2014, Abecasis *et al.* 2015, Zupan *et al.* 2018). Our results show that buffer zones of western Mediterranean MPAs are being effective for the conservation of predatory fish, thus acting as a promising way of management of the resources (Chapter II). The Mediterranean Sea is a highly crowded sea, and many ways of live have traditionally been linked to the sea, such as the fisheries industry and the tourism (Prato *et al.* 2013). In such situation, the implementation of large no-take zones would lead to strong social conflicts. Hence, MPAs consisting on small no-take zones (Giakoumi *et al.* 2017) and buffer zones act as multiple use zones, which is especially important because allow the conservation of the resources as well as the maintenance of some activities, which are strongly regulated (Di Franco *et al.* 2016).

Cabo de Palos-Islas Hormigas MPA is one of the most effective MPAs in the western Mediterranean Sea (Goñi *et al.* 2008, Hackradt *et al.* 2014). Our results show that long term protection is necessary for achieving the recovery of predatory populations. However, the lack of surveillance in a period due to economic constraints prevented from identifying the real carrying capacity (Chapter II). Temporal trends in Chapter II indicate that predatory fish achieve carrying capacities when the whole period is analysed, but keep increasing exponentially when accounting for the period in which surveillance was high and constant. The importance of achieving a high enforcement in essential for the correct functioning of MPAs, as previously highlighted. Here, we empirically evaluated the effect of the lack in surveillance and concluded that temporal patterns may be different when surveillance is in force. Moreover, although Cabo de Palos-Islas Hormigas MPA cannot be considered a pristine ecosystem, due to the lack of species that traditionally were in the area, the high biomass and density of fish, particularly predatory fish, indicate that well managed MPAs can provide enormous ecological benefits to these populations. Moreover, the fact that a possible top-down process has been identified in the area is of great importance, as the overfishing of predatory species prevents from observing this pattern in nature. However, other environmental or biological factors occurring in the area come together to provide an additional explanation for the disproportionately high biomass values found in this MPA, so that local primary production, the unique habitat structure, the occurrence of external energy subsidies, the dynamics of the early stages of the species life cycle, or even biases due to the average depth at which sampling has been carried out, can be called on to explain the values obtained.

Additionally, many efforts have been made to understand the best methodological approaches to gather reliable information on fish populations (Edgar *et al.* 2004, Prato *et al.* 2017, Irigoyen *et al.* 2018). Conventional strip transects are the most common methodology used for fish populations evaluation, and may be useful to evaluate MPA performance by comparing different levels of protection (Harmelin 1987, García-Rubies & Zabala 1990, García-Charton *et al.* 2004, Hackradt *et al.* 2014). However, our results from Chapter III show that this methodology may be overestimating fish counts and may not be able to detect some of the species present

in the area, thus estimates of density, biomass, richness and population sizes may be biased. Hence, the values found for carrying capacities may be biased due to the sampling methodology applied, and extra efforts should be apllied to calculate reliable population sizes, particularly through a recalculation based in the results from the TRT+DS methodology. Nevertheless, the maximum density and biomass found in Cabo de Palos-Islas Hormigas MPA are much higher than in other Mediterranean MPAs evaluated with the same methodology, which have been protected for similar times (Chapter II), indicating that Cabo de Palos-Islas Hormigas is a hotspot of biodiversity in the western Mediterranean Sea.

The inclusion of the essential habitats for the species is key to ensure the effectiveness of the MPAs (Sánchez-Carnero *et al.* 2016), as they may allow the occurrence of any life stages of the species by including some or all of their habitat requirements (Gailaduk *et al.* 2018). Our results show that habitats with great complexity are the most selected by the species under scrutiny. Moreover, there are differences among immature and mature individuals, preferring the first shallower areas and the latter deeper zones (Chapter IV). Both Cabo de Palos-Islas Hormigas and Cabo Tiñoso MPAs are located in areas with high habitat suitability for the species. Additionally, the area of Cabo Cope, in the southernmost zone of the Región de Murcia includes high suitable habitats for the distribution of the species. This area is at a short distance from the other studied areas of Cabo Tiñoso and Cabo de Palos-Islas Hormigas MPAs, allowing a high connectivity among them (Calò *et al.* 2016a, 2016b). The implementation of a new small and well enforced MPA in that area would serve as protection of focal species as well as ensuring a good connectivity among MPAs.

Based on our results, we suggest the implementation of small and well enforced MPAs, and located in areas with high bottom complexity, to ensure suitable habitats for the species. Moreover, we suggest the introduction of the TRT+DS methodology as a routine monitoring for the predatory group, which combined with smaller TRT or the CST method would allow for a better assessment of the fish assemblages.

Future perspectives

The present thesis has contributed to increase knowledge of several processes related to predatory fish recovery in MPAs. However, several processes have not been addressed and may contribute to the patterns found, and other tools and perspectives might help to confirm the mechanisms identified in the thesis and their possible explanations. Thus, we propose the following studies in order to complete the information regarding the effects of protection on predatory fish populations.

First, in order to better identify the effects of fishing regulation on the conservation of fish populations it is necessary to include the range of movements that fish perform. The protection of the species depends on the proportion of their home range included in the MPA (Di Franco *et al.* 2018). However, the information regarding species home range is mostly absent or differs across areas. Thus, for a better assessment of the effects of protection extra efforts are necessary to perform further mobility studies and include information regarding species movements.

The fact that Cabo de Palos-Islas Hormigas MPA appears as a hotspot of biodiversity in the Mediterranean Sea could be due to several processes, such as the primary productivity hypothesis, the sampling-depth hypothesis, the habitat-structure hypothesis, the 'supply side' hypothesis, and the energetic-subsidies hypothesis (Chapter II). Several approaches would help to confirm the different proposed hypothesis in the area. For instance, studies focusing on functional (Villéger *et al.* 2017, Rincón-Díaz *et al.* 2018) and tropho-dynamic (Prato *et al.* 2016) modelling of the reserve effect would help to fully understand the changes that have occurred among the trophic groups and functional features of the fish assemblage as a result of protection.

Additionally, variations in early life history stages may partially determine the size of adult populations (Roughgarden *et al.* 1988), and most of the predatory fish species in the area have not been studied yet. Thus, additional multidisciplinary studies on connectivity and early-life history stages of a range of ecologically representative species (i.e. with different life characteristics) would be necessary to portray the

relative contribution of supply-side influence on the dynamics of the fish assemblage in this MPA (Pascual *et al.* 2017).

Moreover, performing diet studies through stable isotopes (Funes *et al.* 2018) would help to explain the resource distribution in this MPA in which the density of predatory fish is enormous. This approach would allow to understand the varying feeding habits among the different species, and evaluate if it is dependent on the location (i.e. differences among Cabo de Palos-Islas Hormigas and Cabo Tiñoso MPAs), thus clarifying the possibility of the energetic-subsidies hypothesis (Shipley *et al.* 2019). Another complementary approach to understand species diet would be through metabarcoding (Heindler *et al.* 2018, Arrizabalaga-Escudero *et al.* 2019, Brassea-Pérez *et al.* 2019), in which DNA is processed to identify different prey species in a sample, and which is a recent approach that allows for studying the feeding habits of key species in ecosystems that are highly productive and susceptible to change (Brassea-Pérez *et al.* 2019). Additionally, trophodynamic modelling (Prato *et al.* 2014) would help to describe ecosystem functioning and structure, and assess the energetic explanations in the food webs in the area.

Results from the different methodologies applied in Chapter III gave varying estimates for the response variables (richness, density and biomass). Data gathered with the TRT+DS appeared more reliable than CSTs, and indeed CST appeared overestimating fish counts. In order to accurately build the trophic pyramid in Cabo de Palos-Islas Hormigas MPA, a correction would be made to counts gathered with CST. Both methodologies assume different premises, but a new working line trying to relate both estimates and apply a correction based in TRT+DS estimates would help to review the maximum values of biomass in Cabo de Palos-Islas Hormigas and other Mediterranean MPAs.

Different species distribution models (SDMs) lead to variable results (Monk *et al.* 2010). While one alternative is to follow the most parsimonious approach in terms of input information (Chapter IV), an alternative would be to apply several algorithms and perform an ensemble model in order to have a more robust statistical approach (França *et al.* 2019, Norberg *et al.* 2019, Thuiller *et al.* 2019). Hence, we propose to

explore this alternative methodology to reanalyze data from Chapter IV. Also, the application of the recent extension of SDMs to describe data recorded for multiple species (referred to as joint species distribution models - jSDMs, Caradima *et al.* 2019, Tobler *et al.* 2019) could be considered as a way to study the co-distribution of several species belonging to the same trophic guild. Moreover, combining home range with SDMs allow for a better understanding of the effects of protection on the species (Abecasis *et al.* 2014), thus including such information would lead to more reliable results.

GENERAL

CONCLUSIONS

Chapter 1: Factors influencing the effectiveness of Marine Protected Areas for the conservation of predatory fish worldwide

1. Overall, marine protected areas provide ecological benefits for piscivorous fish worldwide both in terms of biomass and density. However, the response to protection varies among species and marine protected areas.

2. The effect of protection was stronger for the biomass of medium-sized fishes and the density of large and gregarious species, indicating that vulnerable species are more susceptible to benefit from protection.

3. The size of the no-take zone had a significant negative impact on both response variables and differed according to the level of enforcement, with smaller no-take zones having higher levels of enforcement and providing greater ecological benefits to piscivorous fish.

Chapter 2: Effects of long-term protection on fish populations in the Cabo de Palos-Islas Hormigas Marine Protected Area

4. Overall, biomass of reef fishes increased with time in the Cabo de Palos-Islas Hormigas MPA while the opposite pattern was found for density, suggesting that the MPA harbours less but larger fish.

5. Particularly, piscivorous fish and medium-sized invertebrate feeders increased in the long-term reaching carrying capacities after 10-15 years while the other trophic groups remained constant or diminished, suggesting top-down processes in the area.

6. When accounting only for the period in which enforcement was high and constant, some descriptors, like piscivores, grew exponentially, indicating that continuous enforcement leads to greater increases.

7. Commercial species showed differential responses to protection, thus other biological and ecological features may explain the patterns found, such as the trophic position or the early life stage ecology.

8. Cabo de Palos-Islas Hormigas harbours disproportionately higher biomass of fishes than other Mediterranean MPAs, which could be explained in part by different non-exclusive hypotheses, namely: primary-productivity effect, depth effect, habitat effect, 'supply-side' effect, and/or energetic-subsidies effect.

Chapter 3: Effects of the sampling methodology on the detection of protection benefits on predatory fish

9. Detection of the protection effects on predatory fishes depends on the census methodology applied. Estimators covering larger areas allowed the detection of a greater number of species (i.e. TRT20) than transects of narrower fixed widths. Moreover, estimators covering larger areas yielded more accurate and realistic values of density and biomass (i.e. TRT+DS and TRT20) than transects of narrower fixed widths, particularly the CST.

10. Both no-take zones and buffer zones appeared effective for the conservation of large predatory fishes, indicating that multiple use zones are effective for the conservation of predatory fish.

11. Cabo de Palos and Es Freus were the most effective MPAs, contrary to the case of Menorca, probably due to both environmental factors, such as the primary productivity levels, and management factors, like the level of enforcement.

Chapter 4: Habitat selection of predatory fish in protected and unprotected areas

12. Bathymetry and habitat complexity of predominantly rocky bottoms determined species distribution in the studied areas, either with high or low density of fish, although there were differences in the contribution of the variables at each location. In Cabo de Palos-Islas Hormigas BPI the variables rugosity, slope and terrain ruggedness index contributed the most to species distribution. In Cabo Tiñoso MPA- Cabo Cope

bathymetry position index, curvatures, rugosity, slope, terrain ruggedeness and, contrary to CP, eastness were the most important variables for the distribution of the species.

13. Habitat requirements were different for the immature and mature individuals, generally being the immatures located at shallower areas and being the most sensitive to changes of the habitats.

19. Both MPAs and the unprotected area analysed in this study appeared with areas of high suitability for the studied species, indicating that the MPAs are established in proper areas, and suggesting another area for the establishment of a new MPA to enhance a MPA network in the region.

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